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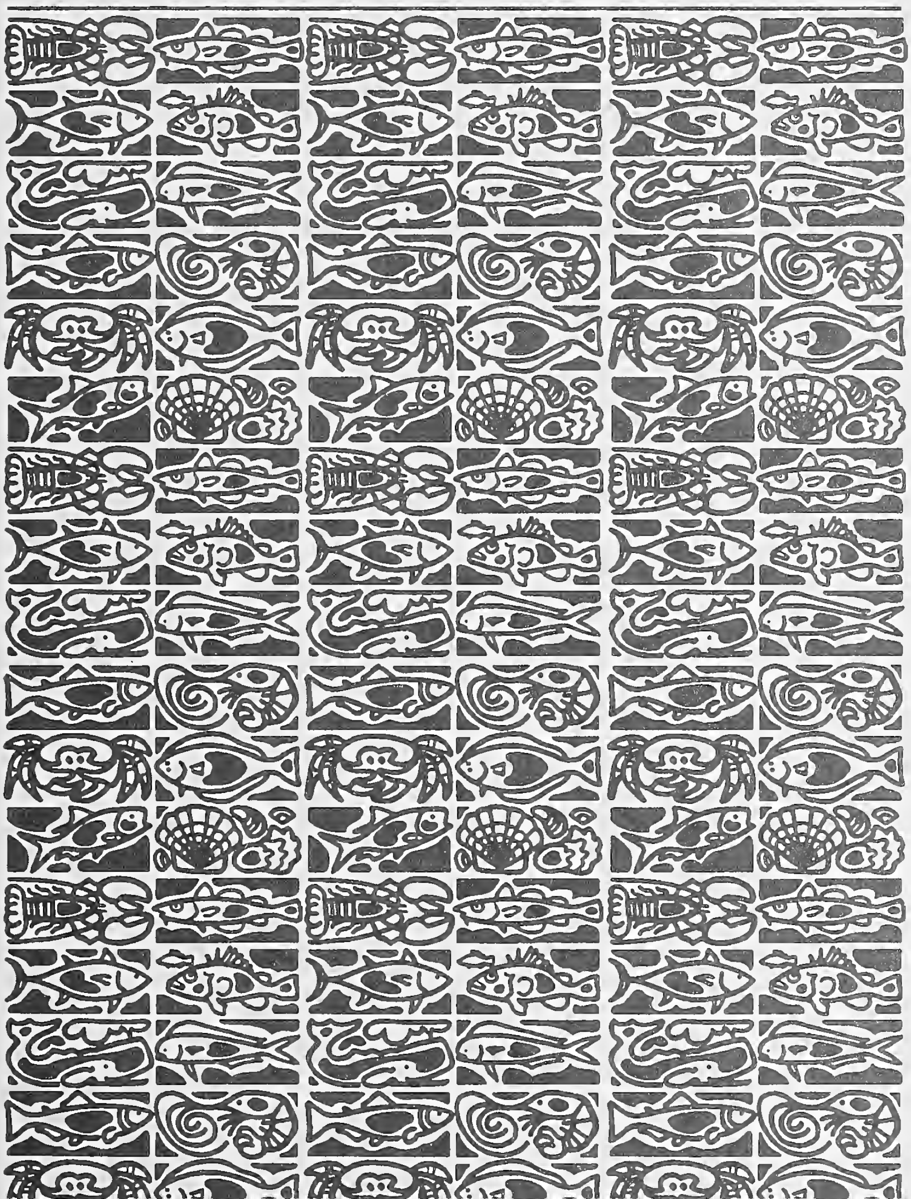

Fishery Bulletin

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Articles

Companion articles

Age and growth of spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska: analysis of alternative growth models

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Abstract—Ten growth models were fitted to age and growth data for spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska. Previous studies of spiny dogfish growth have all fitted the t_0 formulation of the von Bertalanffy model without examination of alternative models. Among the alternatives, we present a new two-phase von Bertalanffy growth model formulation with a logistically scaled k parameter and which estimates L_0. A total of 1602 dogfish were aged from opportunistic collections with longline, rod and reel, set net, and trawling gear in the eastern and central Gulf of Alaska between 2004 and 2007. Ages were estimated from the median band count of three independent readings of the second dorsal spine plus the estimated number of worn bands for worn spines. Owing to a lack of small dogfish in the samples, lengths at age of small individuals were back-calculated from a subsample of 153 dogfish with unworn spines. The von Bertalanffy, two-parameter von Bertalanffy, two-phase von Bertalanffy, Gompertz, two-parameter Gompertz, and logistic models were fitted to length-at-age data for each sex separately, both with and without back-calculated lengths at age. The two-phase von Bertalanffy growth model produced the statistically best fit for both sexes of Gulf of Alaska spiny dogfish, resulting in L_∞=87.2 and 102.5 cm and k=0.106 and 0.058 for males and females, respectively.

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The spiny dogfish (*Squalus acanthias*) is a small long-lived shark common among temperate coastal areas in the Atlantic and Pacific oceans (Compagno, 1984). This species has been the target of commercial fisheries over much of its range, in some cases for over a century (Ketchen, 1986). In some areas, severe declines in population abundance and stock structure have occurred (e.g., Rago et al., 1998). Many elasmobranchs, including spiny dogfish, are "equilibrium strategists" that are highly susceptible to overfishing because of their slow growth rates, low fecundity, and late maturation (King and McFarlane, 2003), all of which are directly related to recruitment and parental stock sizes (Holden, 1974; 1977). Off the west coast of North America, spiny dogfish were depleted by intense fisheries in the 1940s, owing to the quantity and quality of vitamin A in their livers (Ketchen, 1986); the fishery demand decreased by 1950 with the development of synthetic vitamin A (Ketchen et al., 1983). Since the 1970s, spiny dogfish have continued to be targeted by commercial fisheries in British Columbia and the state of Washington for human consumption.

Although not targeted, spiny dogfish is a common bycatch species in many fisheries in both state and federal waters off the coast of Alaska. In the Gulf of Alaska (GOA) spiny dogfish are taken in Pacific salmon (*Oncorhynchus* spp.) gillnet fisheries, sablefish (*Anoplopoma fimbria*) fisheries, Pacific halibut (*Hippoglossus stenolepis*) longline fisheries, and groundfish trawl fisheries (Boldt, 2003). Although an estimated average of 482.1 metric tons (t) of spiny dogfish was taken annually from 1997 to 2007 in observed fisheries (Tribuzio et al., 2008), the bycatch in state waters is unknown and the bycatch rates in federally managed fisheries are likely underestimated because of unobserved fisheries (e.g., the halibut individual fishing quota, IFQ). Nearly all of this unintended bycatch was and still is discarded at sea. Even though estimated catch is <1% of estimated spiny dogfish biomass (Courtney et al., 2006), the potential development of a commercial fishery demands further investigation of the effect of total fishing mortality on biomass and an investigation of spiny dogfish life history characteristics in Alaska.

Biological reference points (e.g., B_{MSY}, $F_{35\%}$) are benchmarks against which stock abundance or fishing mortality rates can be compared to determine stock status. Most commonly used reference points are functions of stock productivity, such as growth, recruitment, and natural mortality (Bonfil, 2005); thus accurate estimates of age and growth are important. For instance, estimates of age and the growth coefficient (k) are critical for estimating natural mortality (M), where a lack of data prevent direct estimation of M, abundance, and appropriate harvest rates. In the GOA, biological reference points, such as those from age and growth models, have yet to be determined for spiny dogfish.

Extension of life history parameters from other regions to Alaska may be inappropriate because age and growth characteristics of spiny dogfish vary widely over its geographic range. For example, maximum age in the northwest Atlantic Ocean is 35–40 years (Nammack et al., 1985), but in the eastern North Pacific, spiny dogfish have been aged to over 80 years (Saunders and McFarlane, 1993). Growth characteristics also vary widely throughout the North Pacific and North Atlantic oceans (Ketchen, 1975; Nammack et al., 1985). Even within the North Pacific basin, biological parameters, such as k, can vary with latitude (Vega, 2006).

The selection of an appropriate growth model is important when estimating regionally specific parameters. Elasmobranch age and growth studies have generally focused on fitting length-at-age data to the von Bertalanffy (vB) growth equation, irrespective of goodness-of-fit or alternative growth models (Carlson and Baremore, 2005). Despite its common use, the vB growth equation may not be the best-fit growth model for all elasmobranch species. For example, the logistic model fitted best among four models tested for the spinner shark (*Carcharhinus brevipinna*, Carlson and Baremore, 2005), and a two-phase vB model fitted best among five models for the piked spurdog (*Squalus megalops*, Braccini et al., 2007). A model that is not the best descriptor of a species' growth could have compounding effects on demographic analyses, stock assessment, and fishery management.

Typical growth models involve parameters of asymptotic length (L_∞), k, and t_0 (Cailliet et al., 2006). The t_0 parameter is biologically difficult to interpret because it is not measurable and testable in wild animals (Beverton and Holt, 1957). This parameter is the age at which the animal is of zero length and is based on an assumption of a fixed growth curve from fertilization through life (Beverton and Holt, 1957). It is generally interpreted to represent the period of gestation in teleost fish species, but this assumption is violated for elasmobranchs (Driggers et al., 2004). For instance, when considering males and females separately, models will estimate different t_0 values. If t_0 is truly representative of gestation time, then it leads to the incorrect inference that male and female pups have different gestation periods. For these reasons, growth models that use size at birth (L_0) instead of t_0 may be more appropriate for elasmobranchs (Cailliet and Goldman, 2004).

The purpose of this study was to estimate best-fit growth models for male and female spiny dogfish in the GOA. Resultant growth equations provide critical parameters for a better understanding of spiny dogfish biology, estimation of biological reference points including indirect estimates of M, improved stock assessments, and development of sound fishery management plans for this species in waters off Alaska.

Materials and methods

Sample collection

Spiny dogfish were collected by targeted sampling cruises, state and federal assessment surveys, and opportunistic fishery bycatch samples between July 2004 and April 2007 across the GOA (Fig. 1, Table 1 (delete bold font after placing tables). All spiny dogfish were sexed and length was measured to the nearest centimeter (total length extended=TL_{ext}; total length natural=TL_{nat}; precaudal length=PCL; and fork length=FL; Tribuzio et al., 2009). Here, length measurements are reported as total length extended (TL_{ext}). The posterior dorsal spine was removed and stored frozen for laboratory analyses. In the laboratory, spines were cleaned by thawing, by boiling briefly, and the loose tissue was scraped free. Spines were allowed to dry overnight and then stored in individual paper envelopes for subsequent age reading.

Sampling bias was examined because we sampled with multiple gear types in different locations. To test for potential bias, a chi-squared (χ^2) test was conducted to test for statistically significant ($P<0.05$) differences in the mean length at age by sex for each gear (trawl, setnet, longline, rod and reel) and region (Cook Inlet, Prince William Sound, Yakutat Bay, and Gulf of Alaska). Statistically significant differences among different gears would provide evidence of sampling bias. However, statistically significant differences among different geographic areas would provide equivocal evidence of bias because the possibility of true underlying differences in size distributions by area could not be dismissed.

Age determinations

The posterior dorsal spines were read in the laboratory according to the methods of Ketchen (1975) and Beamish and McFarlane (1985). Each band pair (hereafter termed "band"), consisting of one dark and one light band, was counted as one year or annulus (Cailliet et al., 2006). Aging was conducted by two scientists at the Washington Department of Fish and Wildlife's age laboratory and by the lead author at the University of Alaska Fairbankans. Ease of age reading was categorized from 1 (easiest) to 3 (most difficult). Spines were photographed on a 1×1 mm grid to standardize measurements. All measurements were rounded to the nearest 0.01 mm by using Bersoft

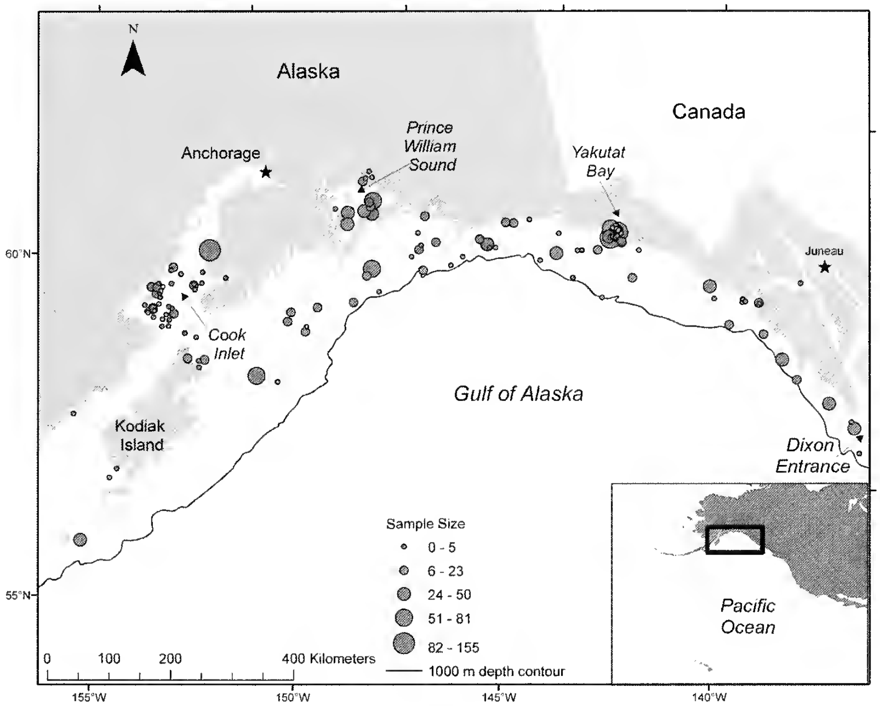

Figure 1

Locations where spiny dogfish (*Squalus acanthias*) were sampled in the Gulf of Alaska in 2004–07. The size of the circle is proportional to the number of spiny dogfish sampled at each location.

Table 1

Locations, gear types, and sample sizes for male and female spiny dogfish (*Squalus acanthias*) collected during 2004–07. "Sport" gear refers to hook-and-line fishing with rod and reel, "longline" refers to multiple hooks on a groundline, "trawl" denotes either bottom or pelagic trawls, and "set net" refers to a stationary floating gill net, generally anchored at one end to the shore.

Year	Area	Gear	Males (*n*)	Females (*n*)
2004	Yakutat Bay	Sport	21	91
2004	Gulf of Alaska (GOA)	Longline	52	85
2005	Southeast Alaska (SEAK)	Longline	1	13
2005	Yakutat Bay	Longline	11	23
2005	Yakutat Bay	Sport	0	15
2005	Cook Inlet	Sport	6	25
2005	Yakutat Bay	Longline	41	95
2005	GOA	Longline	112	204
2005	Cook Inlet	Sport	8	12
2005	Yakutat Bay	Sport	1	72
2005	Prince William Sound	Longline	27	69
2005	GOA	Trawl	83	125
2006	Kamishak Bay	Trawl	24	26
2006	Cook Inlet	Set net	50	90
2006	Copper River	Set net	9	5
2006	Yakutat Bay	Set net	4	57
2006	Icy Point (SEAK)	Trawl	0	1
2006	Prince William Sound	Longline	87	91
2006	Cherikoff Island (SW GOA)	Trawl	28	13
2007	Cherikoff Island (SW GOA)	Trawl	20	16

Image Measurement vers 5.0 software (Bersoft, Inc., http://bersoft.com). Measurements included spine base diameter (*SBD*), enamel base diameter (*EBD*), last readable point (*LRP*, also called the no-wear point); and, for nonworn spines, base length (*BL*), and spine total length (*TL*, Fig. 2) were also measured to the nearest 0.01 mm. Nonworn spines were those spines with a *LRP*<2.45 mm (McFarlane and King, 2009), which is the *EBD* at birth.

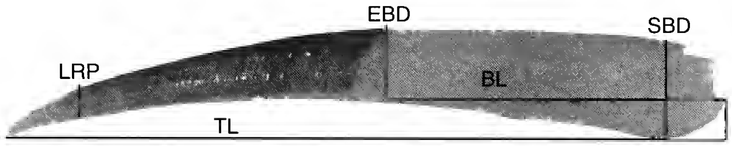

Figure 2

Measurements taken on spiny dogfish (*Squalus acanthias*) spines. Last readable point (LRP) is the point where the bands are no longer visible on the leading edge of the spine (upper edge in this picture). EBD = enamel base diameter, SBD = spine base diameter, BL = base length, and TL = spine total length, which only applies to spines that are unworn. All measurements were taken in millimeters.

Aging bias and precision were evaluated for all three readers. Pair-wise age-bias plots were used to compare each reader against the other two (Campana et al., 1995) and a χ^2 test for symmetry was used to test for statistically significant systematic bias among the three readers (Hoenig et al., 1995). Readers were considered to be in agreement when ages were within 10% of each other rather than within some fixed 1- or 2-year age interval. For instance, if reader X counted 10 bands, then reader Y's count would have to have been between 9–11 bands to be in agreement, but if reader X counted 40 bands, then reader Y's count would have to be between 36–44 to be in agreement. We contend that the use of a percentage to define the interval size is more appropriate for this long-lived species. Finally, the coefficient of variation (CV) between readers was calculated according to Campana's methods (2001).

Spiny dogfish ages are not always equal to the number of counted bands for two reasons: 1) bands are deposited during embryonic development, and 2) because the external spines can become worn or can break off. This problem was addressed by a correction method for estimating the number of missing bands that was based on a regression of band counts on the *SBD* of unworn spines (Ketchen, 1975). This method was subsequently re-examined and accepted as the best available method for the original samples plus additional samples from the same geographic region (McFarlane and King, 2009).

Various regression approaches were compared to determine which method resulted in the best model for estimating the number of worn bands in spiny dogfish collected from the GOA, including: nonlinear least squares regression (NLS, Eq. 1), and ordinary least squares (OLS, Eq. 2):

$$Band\ count = b_0 EBD^{b_1} \qquad (1)$$

$$\ln(Band\ count) = \ln(b_0) + \ln(EBD)b_1, \qquad (2)$$

where b_0 and b_1 are estimated parameters (based on Ketchen 1975, McFarlane and King 2009). Also, we fitted parameters for Equations. 1 and 2 with weighted nonlinear least squares (WNLS) and weighted ordinary least squares (WOLS), where weights were applied to the residuals as follows: spines in readability category 1 were given a weight of 1, those in category 2 were weighted by 0.5, and those in category 3 by 0.3. These values were chosen to discount the contribution of individual length at-age data points to the estimation process based on the degree of uncertainty in the age estimates for difficult-to-read spines. As an alternative to this weighting scheme, we explored the weighting process by using the inverse of the variance in assigned ages for each readability category. Ages of worn spines were then estimated by equating the *LRP* to the *EBD* in the best-fit model from Equations 1–4 and by adding the resultant number of bands to the median band count from the three readings and by subtracting two years (for bands deposited during gestation) to obtain the final estimated age of the animal (Ketchen, 1975). In the case of nonworn spines, age was estimated by the median band count minus two years. Data for males and females were combined for these worn band models.

Fitting of growth models

A total of 10 growth model variations were fitted separately to the length-at-age data for males and females (Table 2). The growth models included 1) the vB growth model for estimating t_0; 2) the two-parameter vB with fixed L_0; 3) the two-phase vB with L_0 (used in the present study); 4) the Gompertz; 5) the two-parameter Gompertz; and 6) the logistic. For comparison with previous studies L_0 is estimated for model 1 by setting $t=0$. An estimate of L_0 (i.e., the size at birth) for GOA spiny dogfish was not available; therefore model 2 was run with L_0 fixed at 26.2 cm (size at birth for spiny dogfish from British Columbia; Ketchen, 1972). Models 3 and 5 were run in three different ways: 1) L_0 was estimated by the model; 2) with L_0 set at the value estimated from model 1; and 3) with L_0 set at 26.2 cm. Model 3 is an adaptation of the two-phase vB model (Soriano et al., 1992). Standard fitting procedures with the two-phase model resulted in the A_t parameter from Soriano et al. (1992) changing for a brief time period and then returning to its original value. To correct this we reformulated the A_t parameter from Soriano et al. (1992); this treatment changes k, depending on the age of the dogfish, so that A_t would

Table 2

Growth models fitted to spiny dogfish (*Squalus acanthias*) length-at-age (L_t) data. Parameters are: asymptotic length (L_∞), the growth coefficient (k), length at birth (L_0), age at size zero (t_0), a phase change parameter (A_t) for the two-phase model, age at transition (t_h), magnitude of the maximum difference between model 1 and the two phase model (h), time increment from previous t value (δ), and the inflection point of the logistic curve (a).

Model number	Model name	Model equation	Reference
1	vB 1	$L_t = L_\infty\left(1-e^{-k(t-t_0)}\right)$	von Bertalanffy (1938)
2	vB 2	$L_t = L_\infty - \left(L_\infty - L_0\right)e^{-kt}$	Fabens (1965)
3a–3c	Two-phase vB with L_0	$L_t = L_{t-\delta} + \left(L_\infty - L_{t-\delta}\right) * \left(1-e^{-A_{t-\delta}k(t-t_{t-\delta})}\right),$	This study
		$A_t = 1 - \dfrac{h}{1+e^{slope(t_h-t)}}$	
4	Gompertz	$L_t = L_\infty e^{-e^{\left(-k(t-t_0)\right)}}$	Ricker (1975)
5a–5c	Two-parameter Gompertz	$L_t = L_0 e^{G\left(1-e^{-kt}\right)}, G = \ln\dfrac{L_\infty}{L_0}$	Mollet et al. (2002)
6	Logistic	$L_t = \dfrac{L_\infty}{1+e^{-k(t-a)}}$	Ricker (1979)

follow a logistic pattern and remain in the second phase. Another problem we encountered fitting the two-phase model was that the typical differential form of the vB equation can result in a decrease in length at the transition between phases. To prevent this unlikely result the difference equation form of the vB equation (Gulland 1969) was used in this analysis.

Model parameters for equations describing the number of worn bands or growth were fitted by nonlinear least-squares regression or ordinary least-squares regression, and confidence intervals were estimated by a bootstrap procedure with 5000 replicates by using R statistical software (R, vers. 2.10.0, www.r-project.org). Confidence intervals (95%) for parameter estimates were based on the lower and upper 2.5th percentile of the bootstrap replications. Parameters were considered significantly different if the 95% confidence intervals did not overlap. To evaluate best model fit for the male and female datasets, Akaike information criteria (AIC) and model summary statistics were calculated (Burnham and Anderson, 2004).

Back-calculation methods

Owing to a paucity of specimens with $EBD<3.5$ mm, back-calculation methods were used to fill in the size range missing from samples. The spine diameter at each band along the spine (hereafter called "band diameters") was measured from a random subsample of 153 unworn spines for use in the estimation of worn bands (Eqs. 1–4); spiny dogfish with unworn spines tend to be smaller and younger than those with worn spines. We examined the Dahl-Lea, linear Dahl-Lea, and size at birth modified Fraser-Lee back-calculation methods (Francis, 1990; Campana, 1990; Goldman et al., 2006). The Fraser-Lee method produced results that on an individual level could be quite unreasonable (large negative ages), but on average were more biologically reasonable than either of the Dahl-Lea methods. Further, growth model results with either of the Dahl-Lea methods were unreasonable (L_∞ of >150 cm TL_{ext}), therefore, we used the Fraser-Lee method for our data. Thus, the following equation was used to estimate back-calculated length-at-age data:

$$TL_i = TL_c + \frac{\left(EBD_i - EBD_c\right)\left(TL_c - TL_{birth}\right)}{EBD_c - EBD_{birth}}, \tag{3}$$

where TL_i = the back calculated length;
TL_c = the length at capture;
TL_{birth} = the length at birth;
EBD_i = the enamel base diameter at band I;
EBD_c = the enamel base diameter at capture; and
EBD_{birth} = the enamel base diameter at birth.

Results

Sample collection

A total of 1713 spiny dogfish were sampled over the four years of the study (585 males, 1128 females, Table 1) of which 537 male and 1062 female spines were usable. Lengths ranged from 56 to 99 cm TL_{ext} for males, and 56 to 123 cm TL_{ext} for females. The χ^2 test revealed no significant differences between the mean length at age

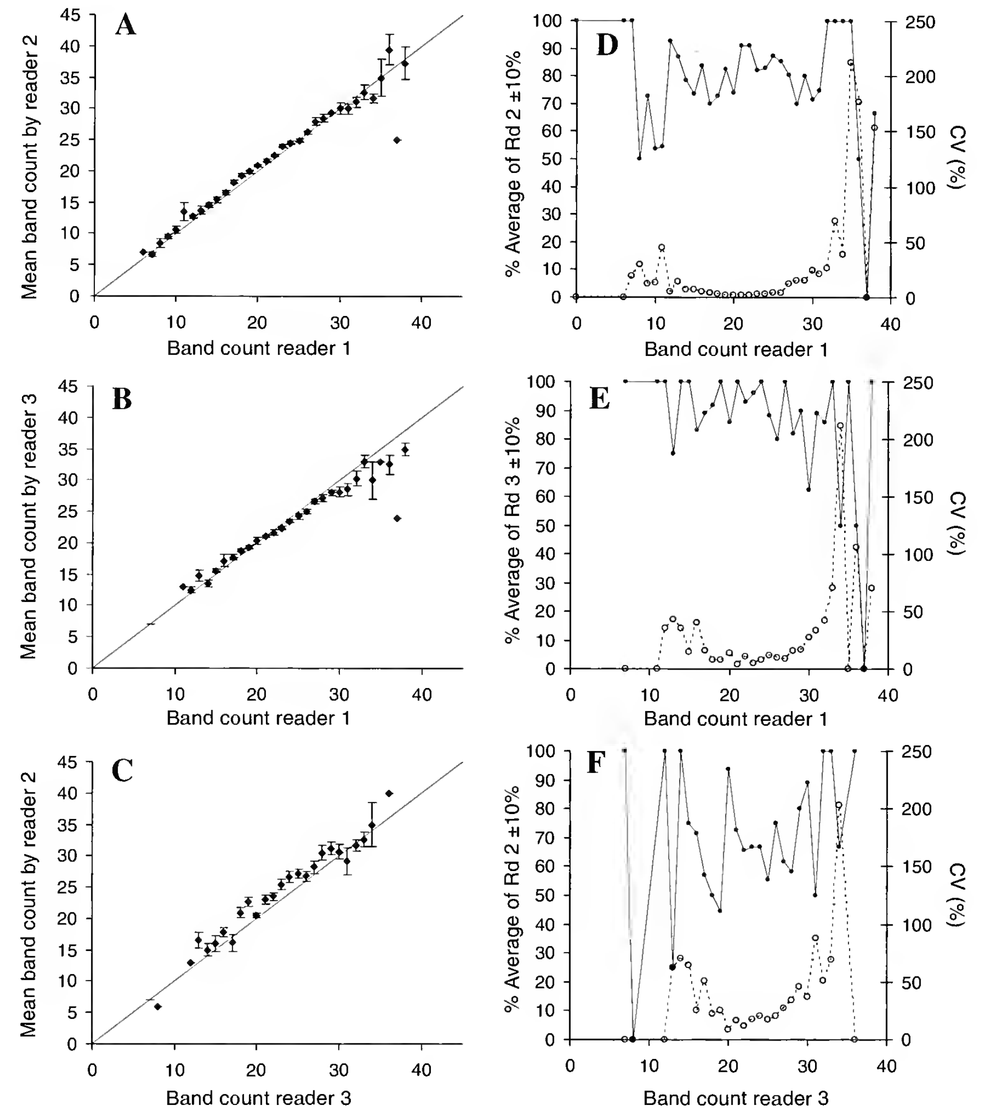

Figure 3

A comparison of age counts among readers. (**A**) Reader 2's mean band counts (y-axis) in relation to the band counts of reader 1; (**B**) Reader 3's mean band counts in relation to the band counts of reader 1; and (**C**) Reader 2's mean band counts in relation to the band counts of reader 3. Vertical lines are 95% confidence intervals and the diagonal line is the 1:1 relationship line. (**D**) Percent agreement and coefficient of variation for reader 2 (Rd 2) compared to reader 1. The percent agreement (±10%) is represented by the solid line and circles and the coefficient of variation (CV) by the dashed line and open circles. (**E**) Percent agreement and coefficient of variation of reader 3 (Rd 3) compared to reader 1; and (**F**) Percent agreement and coefficient of variation of reader 2 (Rd 2) compared to those of reader 3.

of any of the data groupings ($P>0.99$, $0.019<\chi^2<4.525$). Thus, we failed to find evidence of sampling bias or geographic differences in average size at age.

Age determinations

Sampled dogfish ranged in age from 8 to 50 years old. The χ^2 test and the age-bias plots indicated no significant systematic bias between the three readers (χ^2=241, 206, and 259 between readers 2 and 1, readers 2 and 3, and readers 3 and 1, respectively; all $P>0.05$; Fig. 3, A–C). The percent agreement between readers 2 and 1 (Fig. 3D) and readers 3 and 1 (Fig. 3E) was high for band counts less than 30 but was more variable or decreased for band counts greater than 30 (Fig. 3, D–F). For readers 2 and 3, the percent agreement was

Table 3

Summary of the parameters used in the worn-band estimation models and model fits for spiny dogfish (*Squalus acanthias*). The observed data are sample data, the band-diameter data were determined from a subsample of unworn spines where the diameter of each band was measured to simulate bound count at spine size for younger animals that were not sampled in this study. Regression models are ordinary least squares (OLS), weighted ordinary least squares (WOLS), nonlinear least squares (NLS) and weighted nonlinear least squares (WNLS). Estimated model parameters (95% confidence intervals in parentheses) and goodness-of-fit indicator AIC, the Akaike information criteria.

		Observed sample data n=685		Observed band-diameter data n=3877	
Model	Parameter	Estimate	AIC	Estimate	AIC
OLS	b_0	2.690 (1.952–3.708)	6.205	0.211 (0.199–0.223)	3.738
	b_1	1.135 (0.949–1.322)		2.867 (2.825–2.910)	
WOLS	b_0	2.471 (1.788–3.415)	6.219	0.212 (–0.201–0.224)	3.721
	b_1	1.179 (0.991–1.367)		2.856 (2.814–2.898)	
NLS	b_0	4.325 (3.400–5.444)	4.016	0.539 (0.487–0.594)	3.781
	b_1	0.955 (0.807–1.111)		2.241 (2.178–2.309)	
WNLS	b_0	4.009 (3.106–5.231)	4.018	0.528 (0.475–0.586)	3.763
	b_1	0.998 (0.826–1.164)		2.247 (2.180–2.318)	

more variable for band counts less than 20 (Fig. 3F). The CV between all three readers was generally low (<30%) for band counts less than 30, and there was a notable increase in the variability and CV for band counts greater than 30.

Spiny dogfish spines grow in a predictable pattern with age (Fig. 4). The brownish-black banded, enameled portion of the spine grows in length at a faster rate than the white base portion.

Inclusion of the back-calculated band diameter data dramatically changed the worn band estimation models (Fig. 5), and therefore further worn band estimations were made with both the observed and back-calculated band diameter data. There were no significant differences between the estimated worn-band model parameters, but the WOLS model had the lowest AIC value and therefore was chosen as the best-fit model (Table 3). Alternative fits to the WOLS and WLNS models, based on weightings by using the inverse variance in assigned ages for each readability category, yielded very similar parameter values and nominally poorer fits indicated by slightly larger AIC values (not shown). A high degree of natural variation resulted in wide 95% confidence intervals for all parameters. Moreover, parameter confidence intervals for the WOLS GOA model widely overlapped the parameter confidence intervals for the Hecate Strait and Strait of Georgia models (McFarlane and King, 2009). Although the parameters were not statistically significantly different, the GOA, Hecate Strait, and Strait of Georgia models appear to represent biologically meaningful differences in growth (Fig. 5). The Hecate Strait and Strait of Georgia models tend to overestimate the band count for larger spines and underestimate for smaller spines of spiny dogfish collected from the GOA.

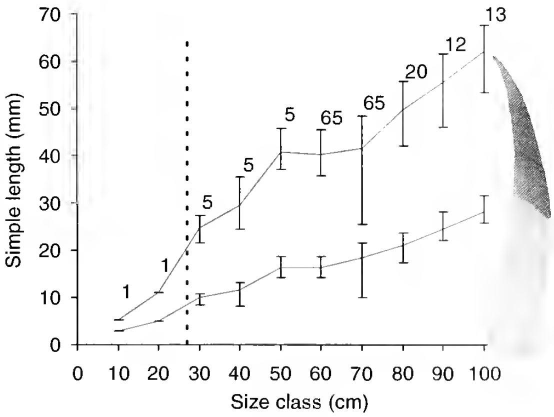

Figure 4

Relationship between mean second dorsal spine length and fish size determined from unworn spines from spiny dogfish (*Squalus acanthias*) collected in the Gulf of Alaska. The top line is spine total length (*TL*) and bottom line is base length (*BL*) in millimeters. Numbers above upper line represent the sample size for each 10-cm size class. Solid vertical lines represent 95% confidence intervals. The dashed vertical line represents the approximate size at birth (Ketchen, 1972).

Fitting of growth models

The two-phase vB models fitted the observed data best for males and females based on AIC values (Fig. 6, A and D, Tables 4 and 5). For males, the two-phase model, where L_0 was used from model 1 (model 3b), was the best fit and for females, it was the model where L_0 was estimated from model 1 (model 3b). Estimated (and 95%

confidence limits) asymptotic lengths (L_∞) were 87.2 cm (range 85.3–90.0 cm) and 102.5 cm (range 99.9–106.3 cm) and growth coefficients (k) were 0.106 (range 0.097–0.117) and 0.058 (range 0.052–0.063) for males and females, respectively. After including the back-calculated data and the mean back-calculated data, the two phase models were no longer the best fit for males. The best-fit model with inclusion of back-calculated data was model 2, and model 1 fitted best for the data including the mean back-calculated data. Similarly, for females the two-phase models were not the best-fit based on AIC values after the inclusion of back-calculated and mean back-calculated data: model 6 was the best fit with inclusion of back-calculated data, and model 5c (with L_0 from model 1) was the best fit for the data including the mean back-calculated data (Tables 4 and 5, Fig. 6, B, C, E, F).

Predicted length at age was similar for males and females for the observed data, up to about age 15, when a transition between growth phases occurred (Fig. 6). After the transition, females continued to grow at a faster rate and to larger sizes than males (Fig. 6, A and D). At the point of transition in the two-phase models growth increased for about five years before slowing, for both sexes.

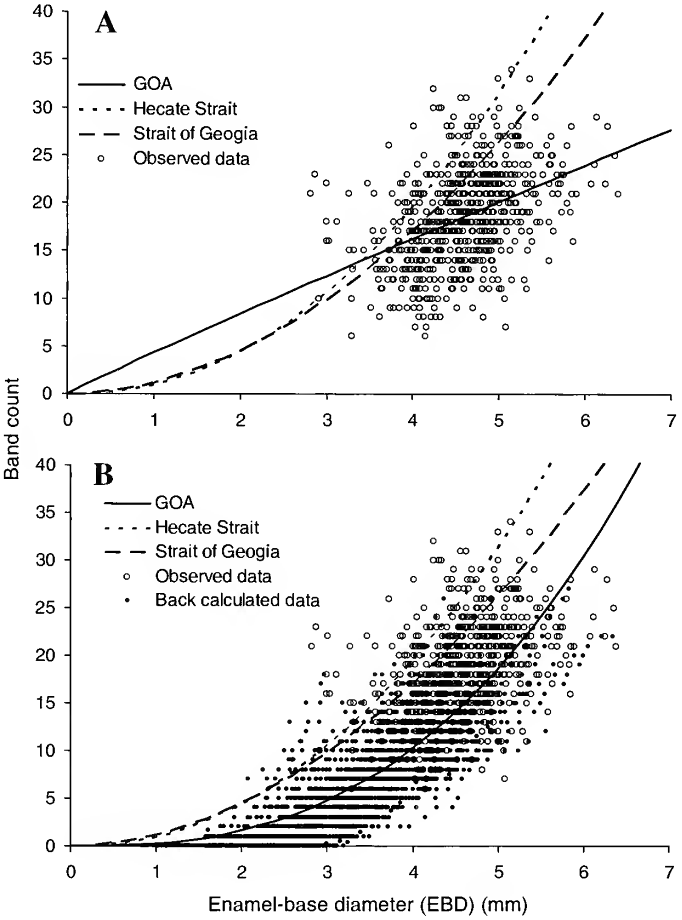

Figure 5

Relationship of band count to enamel-base diameter for spiny dogfish (*Squalus acanthias*) collected in the Gulf of Alaska (GOA) between 2004 and 2007. The best-fit model (weighted ordinary least squares [WOLS]) for (**A**) the observed data only and (**B**) the observed data with the band-diameter data; both sections A and B show the published best-fit relationships for spiny dogfish collected from Hecate Strait and the Strait of Georgia, British Columbia (McFarlane and King, 2009) for comparison.

Discussion

The model fits for all 10 examined growth models were similar and had very small differences in AIC, but the estimated parameters differed substantially; for example, the growth coefficient (k) was significantly different between some models and thus could impact estimates of natural mortality and subsequent demographic analyses. The values of k tended to fall into two groupings (in both data sets), and those models that estimated the higher k were also those that estimated lower estimates for L_∞. Interestingly, even with the significantly different estimates of k, these estimates were still at the lower range of reported growth rates for different types of shark species (Cailliet and Goldman, 2004).

Cailliet et al. (2006) recommended considering more than one form of evaluation of model performance and considering biological interpretations along with statistical fit when choosing the best model. Mean squared error and the correlation coefficient (r^2) were also calculated for each model, but determinations of best fit by the above criteria did not differ from those where AIC was used and therefore are not reported. For the observed data models 3a and 3b were the statistical best fit for males and females, respectively. However, the two-phase models tended to be unstable and would converge at different localized minima, depending on the starting value. A further consideration for the two-phase models is that the growth curve indicates a period of rapid growth immediately following the age at transition.

The purpose of a two-phase model is to incorporate changes in energy allocation as animals grow: immature fish use surplus energy for growth, whereas mature fish use surplus energy for reproduction (Soriano et al., 1992). Thus, the rate of growth changes after maturation. In our case, the transition between the two growth phases occurred before the age at 50% maturity for both males and females The early age at transition and the period of rapid growth after transition indicate that for female spiny dogfish there is a "growth spurt" about 15 years before age at 50% maturity. For

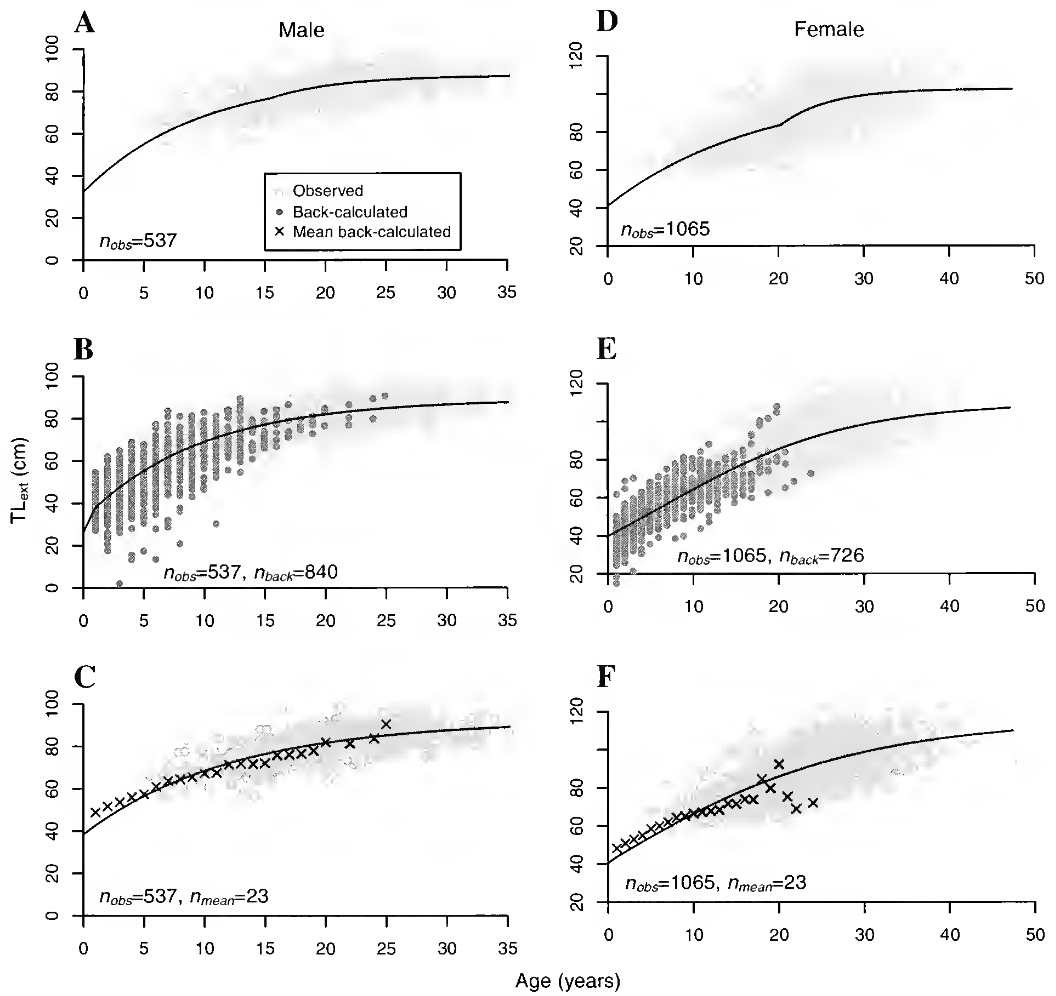

Figure 6

Model fits for male (**A–C**) and female (**D–F**) spiny dogfish (*Squalus acanthias*) length-at-age data. (A and D) Best-fit growth models based on the observed sample data; (B and E) best-fit growth models based on the observed sample data and the back-calculated data; and (D and F) best-fit growth models based on the observed sample data and the mean back-calculated data. n_{obs} is the number of samples, n_{back} is the number of data points created through back calculation of the ages from band-diameter data, and n_{mean} is the number of mean back-calculated data points.

males, the pattern was similar, but occurred just before age at 50% maturity. This finding does not follow the theory behind the two-phase model and indicates that a two-phase model may not be most appropriate in this situation.

The two-phase vB model by Soriano et al. (1992) has been examined with data sets from many species of sharks to determine whether it is an adequate descriptor of shark growth (Araya and Cubillos, 2006). Whereas the two-phase model was better than the standard vB model in 8 of 11 species for females and 7 of 11 for males, the two-phase model did not perform better than the vB (model 1 here) for spiny dogfish. Because Araya and Cubillos (2006) included only one spiny dogfish population (Black Sea), which appears to have different age and growth characteristics from those in the GOA, and only examined average length at age data (Avsar, 2001), we felt that it was worth while to investigate the two-phase family of models in this study. Braccini et al. (2007) found that the two-phase model was the best statistical fit for the piked spurdog, which is a species similar to spiny dogfish; however, the resultant models showed some of the same characteristic difficulties that we encountered. Those results also indicated a decrease in length after transition (Fig. 7, Braccini et al. 2007) and that the A_t parameter appears to change only briefly before returning to its original value. Braccini et al. did not address these issues as we have attempted here. A more comprehensive examination, which would include multiple data sets from different regions for

Table 4

Summary of male growth model results for spiny dogfish (*Squalus acanthias*). The "Observe data" were the actual age at length data from individual spines, the "With back-calculated data" were the observed data with the estimated back-calculated size-at-age data and the "With mean back-calculated data" were the observed data with the mean size-at-age from the back-calculated data. Estimated model parameters with 95% confidence intervals in parentheses and Akaike information criteria, AIC. Asymptotic length (L_∞) and size at birth (L_0) are in centimeters. The growth coefficient (k) and the theoretic age-at-size length zero (t_0) are not reported with units. In model 1, L_0 was solved for by setting t_0=0, this allowed for comparison with other studies.

			Observed data n=537		With back-calculated data n=1377		With mean back-calculated data n=562	
Model number	Model equation	Parameter	Estimate (95% CI)	AIC	Estimate (95% CI)	AIC	Estimate (95% CI)	AIC
1	$L_t = L_\infty\left(1-e^{-k(t-t_0)}\right)$	L_∞	88.3 (87.0–89.7)	4.545	94.5 (92.0–97.6)	4.476	92.1 (89.5–95.6)	4.436
		k	0.095 (0.083–0.107)		0.076 (0.068–0.085)		0.082 (0.065–0.099)	
		t_0	–4.8 (–6.5–3.4)		–5.6 (–6.3–4.9)		–6.6 (–9.4–4.5)	
		Calculated L_0	32.3 (27.4–36.3)		32.7 (32.1–33.2)		38.4 (34.4–40.9)	
2	L_0=*26.2*	L_∞	87.7 (86.6–88.8)	4.474	89.3 (87.8–90.9)	4.435	89.2 (87.9–90.6)	4.457
	$L_t = L_\infty-\left(L_\infty-L_0\right)e^{-kt}$	k	0.105 (0.098–0.113)		0.104 (0.098–0.110)		0.109 (0.101–0.117)	
3a	$L_t = L_{t-\delta}+\left(L_\infty-L_{t-\delta}\right)*\left(1-e^{-A_{t-\delta}k(t-t_{t-\delta})}\right)$	L_∞	87.6 (85.7–89.5)	5.58	89.3 (86.2–94.9)	4.570	87.5 (85.8–90.4)	4.504
		k	0.062 (0.034–0.085)		0.087 (0.074–0.098)		0.090 (0.072–0.104)	
	$A_t = 1-\dfrac{h}{1+e^{slope(t_h-t)}}$	h	–2.0 (–5.8–1.0)		–0.6 (–2.0–0)		–1.0 (–2.4–0.3)	
		t_h	15.4 (13.5–17.6)		14.3 (10.9–18.1)		15.7 (13.4–17.5)	
		L_0	54.6 (46.0–63.1)		32.5 (31.0–34.0)		40.4 (34.3–46.7)	
3b		L_∞	87.2 (85.3–90.0)	4.472	89.5 (86.4–94.2)	4.565	87.1 (85.8–90.1)	4.507
	L_0=*from model 1*	k	0.106 (0.097–0.117)		0.086 (0.076–0.094)		0.100 (0.087–0.108)	
		h	–0.7 (–2.8–0.2)		–0.6 (–2.1–0.0)		–2.3 (–6.5–0.4)	
		t_h	15.4 (12.2–19.2)		14.3 (10.9–18.2)		20.0 (19.6–20.9)	
3c		L_∞	86.9 (85.1–88.8)	4.490	85.9 (83.9–89.1)	5.549	86.3 (85.1–90.0)	4.526
	L_0=*26.2*	k	0.116 (0.106–0.128)		0.114 (0.101–0.118)		0.121 (0.107–0.128)	
		h	–0.5 (–2.9–0.1)		–1.3 (–6.2–0.1)		–2.6 (–4.6–0.1)	
		t_h	15.4 (12.0–19.7)		16.0 (13.3–19.3)		20.0 (14.7–20.3)	
4		L_∞	87.5 (86.3–88.8)	4.559	90.6 (88.8–92.6)	4.477	90.9 (88.7–93.8)	4.458
	$L_t = L_\infty e^{-e^{\left(-k(t-t_0)\right)}}$	k	0.115 (0.100–0.132)		0.111 (0.102–0.120)		0.099 (0.081–0.119)	
		t_0	–1.1 (–2.7–0.3)		–0.3 (–0.6–0.0)		–2.5 (–4.5–1.0)	
5a		L_∞	87.8 (86.3–88.8)	4.557	90.6 (88.7–92.7)	4.479	90.9 (88.7–93.8)	4.458
	$L_t = L_0 e^{G\left(1-e^{-kt}\right)}$	L_0	36.3 (30.6–41.4)		34.3 (33.0–35.6)		41.8 (36.7–46.5)	
	$G = \ln\dfrac{L_\infty}{L_0}$	k	0.116 (0.100–0.132)		0.111 (0.102–0.121)		0.099 (0.082–0.119)	
5b		L_∞	86.3 (85.4–87.2)	4.570	85.6 (84.5–86.7)	4.515	87.1 (86.1–88.1)	4.492
	L_0=*26.2*	k	0.144 (0.136–0.152)		0.163 (0.156–0.170)		0.154 (0.145–0.163)	
5c		L_∞	87.0 (86.0–87.9)	4.556	89.3 (87.9–90.8)	4.475	89.8 (88.4–91.5)	4.557
	L_0=*from model 1*	k	0.126 (0.119–0.134)		0.121 (0.115–0.127)		0.111 (0.102–0.120)	
6		L_∞	87.1 (86.0–88.5)	4.571	88.5 (87.0–90.1)	4.499	90.0 (88.2–92.6)	4.475
	$L_t = \dfrac{L_\infty}{1+e^{-k(t-a)}}$	k	0.130 (0.111–0.151)		0.146 (0.135–0.157)		0.116 (0.096–0.137)	
		a	1.2 (–0.4–2.6)		2.8 (2.5–3.1)		0.3(–1.1–1.5)	

Table 5

Summary of results from the female growth models for spiny dogfish (*Squalus acanthias*). The "Observed data" were the actual age at length data from individual spines; the "With back-calculated data" were the observed data with the estimated back-calculated size-at-age data;" and the "With mean back-calculated data" were the observed data with the mean size at age from the back-calculated data. Estimated model parameters with 95% confidence intervals in parentheses and Akaike information criteria, AIC. Asymptotic length (L_∞) and size at birth (L_0) are in centimeters. The growth coefficient (k) and the theoretic age-at-size length zero (t_0) are not reported with units. In model 1, L_0 was solved for by setting t_0=0, this allowed for comparison with other studies.

Model number	Model Equations	Parameter	Observed data n=1065 Estimate (95% CI)	Observed data AIC	With back- calculated data n=1791 Estimate (95% CI)	With back- calculated data AIC	With mean back-calculated data n=1090 Estimate (95% CI)	With mean back-calculated data AIC
1	$L_t = L_\infty\left(1-e^{-k(t-t_0)}\right)$	L_∞	121.4 (112.9–137.6)	5.677	128.4 (122.3–136.5)	5.365	128.8 (118.6–148.7)	5.317
		k	0.034 (0.023–0.045)		0.037 (0.032–0.043)		0.036 (0.024–0.047)	
		t_0	–12.1 (–17.9–8.2)		–8.9 (–9.9–8.0)		–10.5 (–15.0–7.2)	
		Calculated L_0	40.9 (38.1–42.5)		36.4 (33.2–39.7)		40.3 (35.9–42.7)	
2	L_0=*26.2*	L_∞	108.9 (106.3–111.9)	5.668	108.0 (106.0–110.2)	5.364	114.2 (110.8–118.1)	5.314
	$L_t = L_\infty-\left(L_\infty-L_0\right)e^{-kt}$	k	0.055 (0.051–0.059)		0.067 (0.063–0.071)	0.057	(0.052–0.062)	
3a	$L_t = L_{t-\delta}+\left(L_\infty-L_{t-\delta}\right)*\left(1-e^{-A_{t-\delta}k(t-t_{t-\delta})}\right)$	L_∞	102.5 (99.9–106.2	5.371	103.8 (100.9–107.8)	5.387	101.7 (99.4–104.9)	5.374
		k	0.053 (0.040–0.064)		0.057 (0.052–0.063)		0.057 (0.048–0.065)	
	$A_t = 1-\frac{h}{1+e^{slope(t_h-t)}}$	h	–2.5 (–4.3–1.5)		–1.5 (–2.4–0.9)		–2.2 (–3.7–1.4)	
		t_h	20.3 (19.2–21.8)		19.4 (18.1–20.6)		20.0 (19.4–20.5)	
		L_0	45.8 (37.5–54.3)		35.6 (34.3–37.0)		42.2 (35.8–48.4)	
3b		L_∞	102.5 (99.9–106.3)	5.371	103.8 (101.5–113.1)	5.387	100.76 (98.8–103.4)	5.374
	L_0=*from model 1*	k	0.058 (0.052–0.063)		0.057 (0.046–0.060)		0.061 (0.056–0.065)	
		h	–2.1 (–3.7–1.2)		–1.7 (–2.5–0.4)		–2.8 (–3.9–1.8)	
		t_h	20.3 (19.2–21.8)		19.8 (15.3–20.6)		20.8 (20.5–20.9)	
3c		L_∞	101.8 (99.2–105.4)	5.389	98.5 (96.5–100.0)	5.395	100.2 (98.2–102.7)	5.390
	L_0=*26.2*	k	0.073 (0.066–0.078)		0.081 (0.075–0.083)		0.076 (0.070–0.080)	
		h=a	–1.4 (–2.9–0.7)		–3.0 (–5.1–1.5)		–2.0 (–3.1–1.1)	
		t_h=$P50$	20.3 (18.8–22.1)		21.3 (20.4–21.9)		20.8 (20.5–20.9)	
4	$L_t = L_\infty e^{-e^{\left(-k(t-t_0)\right)}}$	L_∞	115.7 (109.2–127.4)	5.683	115.7 (112.2–119.9)	5.355	119.5 (112.5–130.5)	5.314
		k	0.048 (0.036–0.060)		0.064 (0.059–0.069)		0.056 (0.043–0.068)	
		t_0	–1.1 (–2.7–0.4)		1.6 (1.2–2.1)		0.3 (–0.8–1.5)	
5a	$L_t = L_0 e^{G\left(1-e^{-kt}\right)}$	L_∞	115.6 (109.3–127.4)	5.681	115.7 (112.2–119.8)	5.355	119.5 (112.7–130.5)	5.314
		L_0	45.0 (40.1–49.9)		38.2 (37.1–39.3)		43.1 (38.4–47.6)	
	$G = \ln\frac{L_\infty}{L_0}$	k	0.048 (0.036–0.060)		0.064 (0.059–0.070)		0.056 (0.043–0.068)	
5b		L_∞	102.4 (101.0–104.0)	5.660	100.1 (98.8–101.3)	5.412	105.9 (103.8–108.0)	5.330
	L_0=*26.2*	k	0.090 (0.086–0.094)		0.115 (0.111–0.120)		0.096 (0.091–0.101)	
5c		L_∞	111.2 (108.1–114.8)	5.539	112.1 (109.7–114.8)	5.410	116.0 (112.2–120.4)	5.309
	L_0=*from model 1*	k	0.060 (0.053–0.061)		0.071 (0.068–0.075)		0.062 (0.057–0.067)	
6	$L_t = \frac{L_\infty}{1+e^{-k(t-a)}}$	L_∞	112.3 (106.9–120.9)	5.687	109.8 (107.2–112.7)	5.352	114.5 (109.3–122.0)	5.310
		k	0.062 (0.049–0.075)		0.091 (0.085–0.097)		0.075 (0.062–0.089)	
		a	5.1 (3.8–607)		6.3 (5.7–6.9)		5.7 (4.7–7.0)	

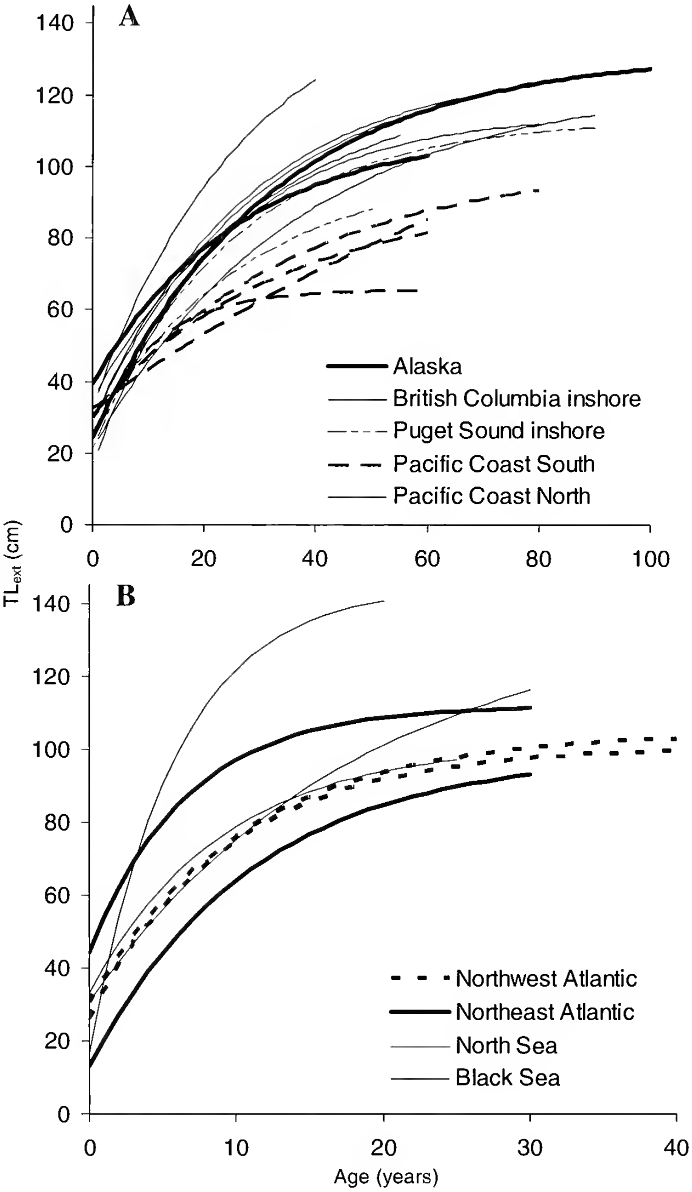

Figure 7

Comparison of published spiny dogfish (*Squalus acanthias*) female growth models from sources listed in Table 4. (**A**) Growth models published for Pacific Ocean spiny dogfish: "Alaska" includes the Gulf of Alaska (GOA) model from this study and a Prince William Sound (PWS) model (Vega, 2006); "British Columbia inshore" includes three models for dogfish sampled within the Strait of Georgia and Hecate Strait (Ketchen, 1975; Saunders and McFarlane, 1993); "Puget Sound inshore" covers models based on samples collected within the Puget Sound area south off British Columbia and east of the Washington coast (Vega, 2006); "Pacific Coast South" includes four models based on samples collected off Oregon and California (Vega, 2006); "Pacific Coast North" includes models based on samples collected off of Washington and the west coast of Vancouver Island (Ketchen, 1975; Jones and Geen, 1977; Vega, 2006); (**B**) The growth models from the Atlantic Ocean, North Sea. and Black Sea (Holden and Meadows, 1962; Sosinski 1978; Nammack et al., 1985; Fahy, 1989; Avsar, 2001; Henderson et al., 2002; Soldat [footnote 1 in Table 6]). Note the different x-axis scales.

each species, and a complete sample of the size range may lead to a more conclusive determination as to which species exhibit two-phase growth.

Disregarding the two-phase models, the best-fit model was model 2 for males and model 5c for females. In this situation, given the lack of data and difficulties with the two-phase models, it may be more appropriate to select the best model not based on the AIC criteria alone, but to also consider the biological soundness of the models. Model 2 (males) and model 5c (females) are the statistical best fit of the more biologically reasonable models. Both of these best-fit models require L_0 as an input, not as an estimated parameter. The lack of data for spiny dogfish <50 cm TLext likely causes the models that estimate L_0 to have difficulty fitting the data and as a result estimate L_0 to be larger than would be expected.

In the majority of published studies on spiny dogfish age and growth the traditional von Bertalanffy model is used. To facilitate a broader comparison of our results with growth parameter estimates for other regions of the geographic distribution of spiny dogfish, we compared parameters estimated from model 1 (Table 4) with growth curves fitted by using the traditional vB formulation, as reported in published studies (Table 5, Fig. 7). Clear differences in spiny dogfish growth exist between the North Pacific and North Atlantic oceans. For instance, we found that male and female dogfish reach larger asymptotic sizes (87.2 and 112.2 cm TL_{ext}, respectively) in the GOA than off the northeastern United States (82.5 and 100.5 cm TL_{ext}, respectively; Nammack et al., 1985). Indeed, virtually all studies have found large differences in growth of spiny dogfish between the North Pacific and North Atlantic (Table 5, Fig. 7). Fish from the North Atlantic tend to grow more rapidly, achieve smaller asymptotic sizes, and have shorter life spans than those from the Pacific. Differences in growth also exist within the Pacific (Table 5, Fig. 7). For example, our GOA growth estimates are similar to those for spiny dog-

Table 6

Summary of von Bertalanffy parameters (model 1) for growth models for female spiny dogfish (*Squalus acanthias*) from the North Pacific and North Atlantic oceans and the North and Black seas. Parameters are asymptotic length (L_∞) size at birth (L_0), growth coefficient (k), and the theoretic age-at-size length zero (t_0). Here, L_0 was solved for from the published parameter estimates for the purposes of comparison.

Location	L_∞	k	t_0	L_0	Reference
Alaska, Gulf of Alaska	121.4	0.034	–12.1	40.9	This study
Alaska, Prince William Sound	110.4	0.038	–11.6	39.4	Vega (2006)
British Columbia, Hecate Strait	125.1	0.031	–10.6	35.0	Ketchen (1975)
British Columbia, Strait of Georgia	129.1	0.034	–7.3	28.4	Ketchen (1975)
British Columbia, Strait of Georgia	114.9	0.044	–3.6	16.8	Saunders and McFarlane (1993)
British Columbia, offshore	128.5	0.036	–6.9	28.3	Jones and Geen (1977)
U.S., inshore (WA north)	113.5	0.04	–5.2	21.3	Vega (2006)
U.S., inshore (WA south)	100.4	0.036	–8.4	26.2	Vega (2006)
U.S., offshore (WA)	123.6	0.027	–6.9	21.0	Vega (2006)
U.S., offshore (WA)	152.9	0.036	–6.7	32.8	Ketchen (1975)
U.S., offshore (OR)	101.9	0.027	–12.7	29.6	Vega (2006)
U.S., offshore (OR and CA combined)	90.9	0.031	–13.0	30.2	Vega (2006)
U.S., offshore (CA north)	158.9	0.009	–25.3	32.4	Vega (2006)
U.S., offshore (CA south)	123.6	0.027	–6.9	21.0	Vega (2006)
Northwest Atlantic (U.S.)	100.5	0.106	–2.9	26.6	Nammack et al. (1985)
Northeast Atlantic (Ireland)	98.8	0.090	–1.6	13.3	Fahy (1989)
Northeast Atlantic (Ireland)	112.0	0.150	–3.4	44.7	Henderson et al. (2002)
Northwest Atlantic	104.5	0.095	–3.7	31.0	Soldat[1]
North Sea	137.1	0.054	–4.7	30.7	Sosinski 1978 (as cited in Avsar, 2001)
North Sea	101.4	0.110	–3.6	33.2	Holden and Meadows (1962)
Black Sea	145.0	0.170	–0.7	16.3	Avsar (2001)

[1] Soldat, V. T. 2002. Spiny dogfish (*Squalus acanthias* L.) of the northwest Atlantic Ocean (NWA). NAFO Sci. Counc. Res Doc 02/84, 33 p.

fish from offshore Washington State waters (Fig. 7) but greater than those caught in inshore Washington State waters (Puget Sound) and British Columbia (Ketchen, 1975; Jones and Geen, 1977; Saunders and McFarlane, 1993; Vega, 2006). The age and growth studies from British Columbia were conducted on spiny dogfish collected in inshore waters (Strait of Georgia and Hecate Strait); therefore the possibility cannot be ruled out that spiny dogfish from the British Columbia offshore region would have growth estimates similar to those of Washington offshore and GOA spiny dogfish. The vB growth model parameter estimates (L_∞ and k) for northern California spiny dogfish (defined as spiny dogfish between Point Conception to the Oregon border; Vega, 2006) were radically different from our results for the GOA, but the fits for California may have been adversely affected by small sample size.

The wide variability in length-at-age contributes to the lack of statistically significant differences among growth models and worn-band estimation models. This variability may be attributable to one or more of the following factors: measurement error in either length or age readings, sampling bias, true underlying variability in growth at age, and misidentification of worn and unworn spines. We considered the potential role of each of these factors.

Measurement error in the length measurements alone is insufficient to explain the relatively large variability in the size-at-age data. Aging errors may take two forms: imprecision and bias. We found no bias among the three readers tested, but imprecision of the band counts among readers could contribute to variability in the size-at-age data, especially for older ages. We used the median band count (from the three readers) to account for reduced precision because this measure of central tendency is less sensitive to outliers than the mean for small sample sizes (Dudewicz and Mishra, 1988). A more thorough analysis of the precision of age estimates for spiny dogfish in the Pacific Ocean revealed the overall coefficient of variation for aging estimates among four laboratories to be 19% (Rice et al., 2009). Systematic bias was found for two of the laboratories (one biased high, the other biased low) in relation to the other two, but relative bias did not always result in statistically different parameters estimated from vB growth curves (Rice et al., 2009).

Age validation is crucial for growth studies to assure that physical structures used for aging are correctly interpreted. For instance, a systematic aging error could result if the periodicity of band formation is not annual. Annual periodicity of band deposition on second dorsal spines was validated for spiny dogfish in British

Columbia (Beamish and McFarlane, 1985; McFarlane and Beamish, 1987). Moreover, radioactive carbon isotopes absorbed into spiny dogfish spines provided age estimates that agree with previous aging results for the British Columbia spiny dogfish (Campana et al., 2006) and verified that periodicity is annual, even at old ages (Campana, 2001). We assumed that this annual periodicity of band formation in spiny dogfish, which was confirmed for this species in British Columbia, also applies to fish from the GOA. Because spiny dogfish from British Columbia have different age characteristics (e.g., worn band curves, Fig. 5) from those of the GOA, it is possible that the pattern of band deposition may also differ.

Sampling bias was considered by examining potential differences in average size at age among gear type and location of capture. Because there were no significant differences among the average size at age with the different gear types used or the areas sampled, we do not believe that sampling bias was a significant factor affecting our results. However, the lack of significant differences in our study should not be misconstrued to rule out considerations of sampling bias in future spiny dogfish studies, because this species may school by size and sex (Nammack et al., 1985; Ketchen, 1986).

In the western North Atlantic Ocean commercial fisheries target the largest and oldest age classes (Rago et al., 1998). Thus, the size-frequency distributions determined from commercial catches may not be representative of the full size range of fish in the population. Moreover, depletion of large old fish from the population by heavy exploitation means that subsequent research surveys may not catch a representative sample of the full size and age ranges of the population. In the GOA, spiny dogfish are taken as bycatch in multiple fisheries. In some cases, dogfish bycatch is largely unaccounted for, owing to the lack of observers on small (<60-ft) vessels, such as those vessels with salmon gill nets, as well as some longline vessels targeting halibut and sablefish, resulting in an unknown level of total fishing mortality (Courtney et al., 2006). However, in the GOA, it is unlikely that the fishing mortality has truncated the size distribution of spiny dogfish because spiny dogfish are not targeted and recent (2006) estimates of spiny dogfish biomass are 80–100% of the estimated theoretical population carrying capacity (Rice, 2007). Therefore, it is unlikely that the fishery has created size-selective impacts that would lead to erroneous selection of the two-phase models as the best-fit models (Braccini et al., 2007).

One limitation of our size-frequency distributions is the absence of spiny dogfish smaller than 50 cm TL_{ext}. The lack of samples from smaller spiny dogfish is likely due to fishery-dependent opportunistic sampling which apparently occurs in areas devoid of juvenile spiny dogfish. Examination of NMFS spring and fall trawl surveys along the U.S. east coast revealed that in spring most juveniles were caught in water between 50 and 150 m deep (range: 7–390 m) in offshore waters from North Carolina to the eastern edge of Georges Bank, whereas in fall most were caught between 25 and 75 m (range: 12–366 m) in various locations, such as on Georges Bank, Nantucket Shoals, and throughout the Gulf of Maine (McMillan and Morse, 1999). Spiny dogfish smaller than 50cm TL_{ext} have been surveyed in both Puget Sound, Washington (Tribuzio et al., 2009), and in the northern Strait of Georgia (McFarlane et al., 2006) by using bottom trawl gear. In this study, we made numerous unsuccessful attempts to capture juvenile dogfish smaller than 50 cm TL_{ext} in the GOA using sport and longline gear in Yakutat Bay, longline gear with small (10/0 circle) hooks in Southeast Alaska (K. Munk, personal commun.[1]), and commercial bottom trawls off Kodiak Island (J. Gauvin, personal commun.[2]).

A missing size group, such as small dogfish in our case, may cause growth models to overestimate t_0 or L_0, thus decreasing the k estimate. Further, this missing size group may have caused the age of transition, t_h, in the two-phase models to be underestimated. Also, the lack of small animals may have limited our ability to discriminate among competing growth models. We used band-diameter data and back-calculated lengths derived from unworn spines to attempt to address this data gap. The inclusion of the band-diameter data greatly improved the worn-band estimation models, but minimally changed the growth models. Few of the estimated growth model parameters based on the back-calculated and mean back-calculated data were significantly different from those estimated from the observed data alone.

Back-calculation methods are designed to be used when sample sizes are small or if sampling has not occurred each month (Cailliet and Goldman, 2004), but in this case it was the entire smaller end of the size range that was being estimated. With the modified Fraser-Lee size-at-birth method, we had to assume that average size at birth was known. We use 26.2 cm, which is based on data collected from spiny dogfish inside the Strait of Georgia, British Columbia (Ketchen 1972). Sizes at birth are reportedly similar for the species across the northern hemisphere, with ranges of 23–30 cm (Ketchen 1972, Tribuzio et al. 2009). We also assumed that 2.45 mm was the spine diameter at birth, based on studies of British Columbia spiny dogfish (McFarlane and King 2009). Because this is an average as well, it is likely that some spines were classified as "unworn" when they were actually "worn." Spines that are classified as "unworn" can lead to underestimating the age, and in the case of the back-calculation resulted in instances where 20 cm or more of growth was predicted in the first year. Back-calculations may not be appropriate for this species when dorsal fin spines are used as aging structures, but may work well if a structure such as vertebrae are used.

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[1] Munk, Kristen. 2007. Alaska Department of Fish and Game, Juneau, AK, 99801.

[2] Gauvin, John. 2007. Gauvin and Associates, LLC. Burien, WA 98166.

The relatively large variability in size at age of spiny dogfish in the GOA could also reflect true underlying variability in growth rates. Individuals experiencing different thermal and feeding histories are expected to have different growth characteristics. It is also conceivable that our samples represent collections of dogfish from multiple, mixed populations. For instance, 4 of 2940 recoveries (0.14%) of spiny dogfish tagged in British Columbia were recovered in Alaska (McFarlane and King, 2003). Because the movements of spiny dogfish from other areas to and from Alaska are unknown, the degree of mixing is uncertain. However, there is no evidence of genetic differentiation in the Northeast Pacific based on analyses of eight microsatellite loci from dogfish sampled from the Bering Sea, the Gulf of Alaska, Strait of Georgia, Puget Sound, and the coasts of Washington, Oregon, and California (Hauser, 2009). Mixtures of spiny dogfish from other areas with growth characteristics that are different from those of Alaska resident dogfish could contribute to the variability in size at age that we observed in the GOA. Nevertheless, the existence of a statistically significant difference in growth rates from different areas of the Northeast Pacific (Vega, 2006; Table 4 this document) indicates that mixing is incomplete.

Our findings have at least two important implications for management of the species. First, for estimation of stock productivity and biological reference points for spiny dogfish in the GOA, it is important to use growth curves that are fitted to size-at-age data from dogfish captured in the GOA. Although alternative growth model parameters were not statistically significantly different from one another in our study, the variation among predicted length may be of biological significance. For instance, the worn-band estimation curves for the GOA and British Columbia resulted in very different estimates of ages (Fig. 5); use of growth curves for British Columbia would result in estimated numbers of worn bands from dogfish spines in the GOA that would be biased low. For example, for a spiny dogfish with a 1.8-mm *EBD*, the GOA model would estimate an age of one year, whereas both of the British Columbia models would estimate an age of four years. A fish with a 6-mm *EBD* would be estimated to be 30 years old by the GOA model and 46 and 37 years old by the two British Columbia models. Such biases in growth estimates may lead to biases in estimates of biological reference points for fishery management.

Second, as in other portions of their range, the largest spiny dogfish are the oldest females. Because commercial fisheries for spiny dogfish select for the largest individuals, fishing mortality rates are disproportionately higher for this reproductive segment of the population. In the Northwest Atlantic Ocean, a sharp increase in landings during 1987–1993 led to a fivefold increase in fishing mortality rates on females from 0.016 to 0.26; and fishing mortality rates exceeding 0.10 on large (≥80-cm) females resulted in negative pup replacement, subsequently leading to stock decline (Rago et al., 1998). Thus, to sustain spiny dogfish in the GOA, fishery management plans should consider not only slow growth rates, low fecundity, and late maturation of this species (King and McFarlane, 2003), but also the potentially disproportionate number of removals of mature females from the stock by commercial fishing by estimating size- and sex-specific fishing mortality rates and biological reference points.

Future research should address the many uncertainties remaining about spiny dogfish biology and life history in Alaska. In particular, results from this study indicate several areas of research needed to improve our understanding of spiny dogfish age and growth. First, although demonstrated for fish captured off British Columbia (Beamish and McFarlane, 1985; McFarlane and Beamish, 1987; Campana et al., 2006), validation of annual band formation, as well as worn-band properties, for spiny dogfish collected from the GOA should be conducted to describe potential sources of bias in the age estimates for spiny dogfish at this northern portion of their range in the Pacific Ocean. Second, the collection of juvenile dogfish (<50 cm) is needed to provide more precise estimates of growth over their full life history, as well as to help identify statistically best-fit growth models. Third, tagging studies, such as those conducted in British Columbia (King and McFarlane, 2003), would help elucidate the degree to which dogfish in Alaska represent mixed stocks with different growth attributes; such tagging results would help to delineate stock boundaries essential for fishery management. Fourth, controlled experiments are necessary to fully examine the selectivity of various fishing gears for spiny dogfish by size and sex. This would be an important preliminary step toward gear standardization, if long-term sampling programs are envisioned for spiny dogfish. Finally, continued sampling of spiny dogfish over small regional scales is necessary to fully evaluate potential geographic differences in growth and resultant parameters (i.e., natural mortality) within the GOA, as well as to more broadly understand the life history of this species in this portion of its range. Although our study would not have been possible without the diversity of low-cost sampling opportunities afforded to us, including the valuable assistance of state and federal agencies and sport and commercial fishermen, further progress will be accelerated by a full-scale, directed field program, which would be more successful at providing an unbiased sample set of spiny dogfish in the waters off Alaska, and which would aid in efforts to build a more detailed stock assessment, and thus models of population dynamics.

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Effective herding of flatfish by cables with minimal seafloor contact

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Abstract—Otter trawls are very effective at capturing flatfish, but they can affect the seafloor ecosystems where they are used. Alaska flatfish trawlers have very long cables (called sweeps) between doors and net to herd fish into the path of the trawl. These sweeps, which ride on and can disturb the seafloor, account for most of the area affected by these trawls and hence a large proportion of the potential for damage to seafloor organisms. We examined modifications to otter trawls, such that disk clusters were installed at 9-m intervals to raise trawl sweeps small distances above the seafloor, greatly reducing the area of direct seafloor contact. A critical consideration was whether flatfish would still be herded effectively by these sweeps. We compared conventional and modified sweeps using a twin trawl system and analyzed the volume and composition of the resulting catches. We tested sweeps raised 5, 7.5, and 10 cm and observed no significant losses of flatfish catch until sweeps were raised 10 cm, and those losses were relatively small (5–10%). No size composition changes were detected in the flatfish catches. Alaska pollock (*Theragra chalcogramma*) were captured at higher rates with two versions of the modified sweeps. Sonar observations of the sweeps in operation and the seafloor after passage confirmed that the area of direct seafloor contact was greatly reduced by the modified sweeps.

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Otter trawling is one of the most effective methods for capturing commercial quantities of flatfish and is the principal method for flatfish harvest in Alaska waters. However, trawl fisheries have received increasing attention for their potential to affect seafloor habitats. Changes to seafloor ecosystems resulting from the passage of trawl gear have been have described in a wide range of studies (Barnes and Thomas, 2005; Lokkeborg, 2005). These include changes to infaunal (Tuck et al., 1998) and epifaunal (Kaiser et al., 1998; Prena et al., 1999; McConnaughey et al., 2000) communities, as well as indirect effects from changes to seafloor structure and resuspension of sediments (Churchill, 1989). The most common response to mitigate these problems has been closures of sensitive areas to trawling. When such areas have rough, rocky substrates, regulations requiring that trawl footrope cross-sections be below a certain size have been used to discourage fishing in these areas; the smaller footropes make nets more vulnerable to damage (Hannah, 2003; Bellman et al., 2005).

Alaskan commercial flatfish fisheries, among the largest in the world, are pursued almost exclusively with demersal otter trawls. (The exception is the fishery for Pacific halibut [*Hippogossus stenolepis*], a large, piscivorous species that is harvested by longlines.) These otter trawls generally use very long cables, herein called "sweeps," that skim the seafloor ahead and to both sides of the trawl net. In Alaska flatfish fisheries, the fishermen have used progressively longer sweeps to increase the width of their gear and, hence, the area from which flatfish are captured. These sweeps now account for the overwhelming majority of the seafloor area swept by these trawlers to capture flatfish. Although these sweeps greatly increase flatfish catches, they also account for most of the negative effects of trawling on the seafloor.

Although some reviews (Kaiser et al., 2007) have recommended development of modified fishing gear to reduce the effects of trawling on seafloor communities, studies that test such gear are just beginning to be published. He (2007) reviewed such efforts for all mobile fishing gears. A substantial effort in Europe focused on modifications for beam trawling (van Marlen et al., 2005). Guyonnet et al. (2008) described tests of modified gear that reduce the contact of the cables between trawl doors and nets with the seafloor. Although their tests were accomplished with different modifications to gear (dangling chain sections attached to neutrally bouyant rope) and in a very different fishery, their concept is very similar to the modifications we tested.

Ryer (2008) has described flatfish behaviors that are important to

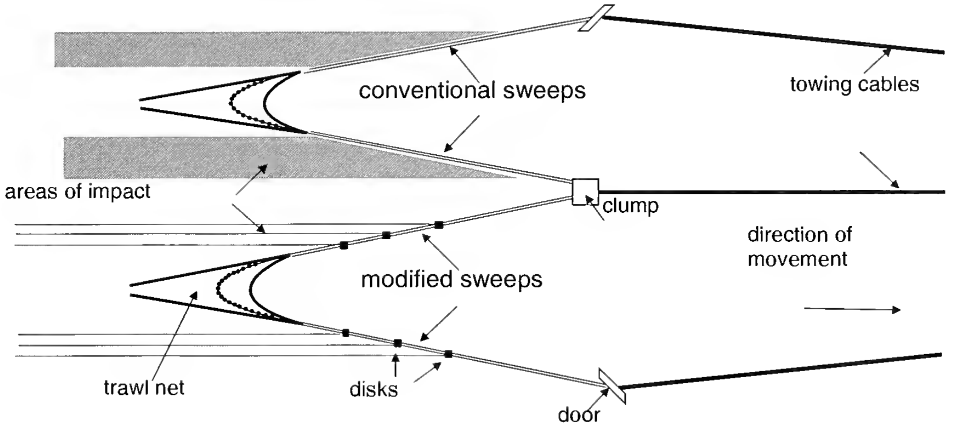

Figure 1

Diagram of the twin trawl system, complete with sweeps (conventional and modified), towed simultaneously behind a vessel and used to test whether raised trawl sweeps reduce flatfish herding. Actual total width was approximately 250 m. Shaded areas represent the area of contact with the seafloor.

their capture by trawls. Flatfish generally react to approaching objects at much closer ranges (<1 m) than do roundfish and remain very close to the seafloor when avoiding such objects. To target these behaviors, towing cables (angled toward the trawl net across the sea floor) are used in both demersal seines and otter trawls to herd flatfish into the path of a capture net. Flatfish avoid the approaching cable by continuous or burst-and-pause swimming, both of which move them gradually into the path of the capture device. Conventional sweep cables have equal diameters throughout, and no structures to interrupt their contact with the seafloor. Here, we test whether effective herding responses could be stimulated if such cables were raised a short distance above the seafloor.

Like most flatfish fisheries, those in Alaska operate on seafloors consisting of unconsolidated mixtures of sand and mud. The potential for reducing damage to the physical and biological features of these habitats by raising sweeps a short distance off the bottom is dependent on the presence of low vertical relief or flexible structures of the bottom relief. This modification would likely not prevent damage to high relief and rigid or fragile features more common on rockier substrates. For the modifications tested here to be effective, their effects on both catch rates and seafloor features need to be examined.

To develop practical modifications for the trawl systems used in Alaska's flatfish fisheries, we convened a series of meetings with trawler captains and gear manufacturers. For initial study, they recommended raising the sweeps slightly above the seafloor, allowing small and flexible animals and other habitat structure to pass beneath. In the current study we examine the proposed change, focusing on determining which adjustments maintain catch rates and on using direct observations to demonstrate reduced seafloor contact.

Methods

To test the effect of the modified sweeps on their ability to herd flatfish, we used a twin trawl system (Fig. 1). A twin trawl system tows two separate trawls, including sweeps, simultaneously on parallel, adjacent tracks. Close proximity and simultaneous operation assure that both nets encounter very similar compositions of fish species at similar abundances. Therefore differences in catch are principally due to differences in the capture effectiveness of the two trawls. The only difference between the trawls in this experiment was the use of the elevating disks on the sweeps of the trawls.

Twin trawl tests

Field experiments were conducted during September 2006 in the eastern Bering Sea onboard the FV *Cape Horn*. The *Cape Horn* is a 47-m trawler processor, active in the mixed groundfish fisheries of the Bering Sea. This vessel was equipped for a twin trawling system, with an extra winch and towing cable. The sweeps and trawls were towed with conventional trawl doors on each side and a weight (clump) in the middle. Both doors and the clump were towed from three separate cables that were adjusted so that both sides fished evenly. Towing sites were selected to provide commercial catch rates of a mixture of the four principal flatfish species of the Bering Sea shelf: yellowfin sole (*Limanda aspera*); northern rock sole (*Lepidopsetta polyxystra*); flathead sole (*Hippoglossoides elassodon*);

and arrowtooth flounder (*Atheresthes stomias*). Towing continued through both day and night periods, reflecting commercial practice. All of the tows were in areas with bottom substrates composed of mixtures of sand and mud (McConnaughey and Smith, 2000).

The trawls were identical two-seam nets with 200-mm mesh in the forward portions and equipped with 130-mm codends. The mouth opening of each net was much wider (25 m) than high (3 m). Similar nets in a single trawl configuration are used to target flatfish on the eastern Bering Sea shelf. The distances between each of the doors and the central clump were monitored for equality with acoustic measurement systems and were each approximately 80 m. Both nets were equipped with sensors that indicated the direction of water flow in relation to the center of the headrope. The three towing cables were adjusted to keep that flow perpendicular to the headropes of both nets and to keep their door-clump openings equal, assuring comparable fishing characteristics for both fishing systems.

The sweeps were 180-m long and were composed of 5-cm (2-inch) diameter combination rope constructed of steel cable covered with polyethylene fiber. This is the most common sweep material currently used in U.S. Bering Sea flatfish fisheries. Sweeps used on vessels to target flatfish on the eastern Bering Sea shelf are 200 to 450 m long (C. Rose, unpubl. data). The sweeps of the two adjacent trawls had to be about half as long as those used with commercial single trawls, because the entire twin trawl system is similar in width to a conventional single trawl. The shorter sweep lengths were necessary to assure that the angle of the test sweeps to the direction of towing was similar to that common in the fishery. In this field study, clusters of disks (disk clusters) were attached over the experimental sweeps at 9-m (30-ft) intervals (Fig. 2). The disks were either 15, 20, or 25 cm (6, 8, or 10 inch) in diameter attached to 5-cm (2 inch) diameter sweeps, creating nominal clearance between the cables and the seafloor of 5, 7.5, and 10 cm (2, 3, and 4 inch), respectively. Nominal clearances are those immediately adjacent to a disk when the disk is resting on a hard surface. The pressing of disks into the seafloor and the sagging of sweeps between elevating devices would affect actual clearances. For stability, disk clusters were approximately the same length as their diameter. These disk clusters were fixed in position with a combination of clamps and rope seizings, which were run through the sweep cable to prevent the clusters from sliding along the cable. Disk clusters were installed on the aft 90 m of the modified sweeps. Halfway through each experiment, the sweeps were switched between the two trawl nets, but each trawl net remained in place.

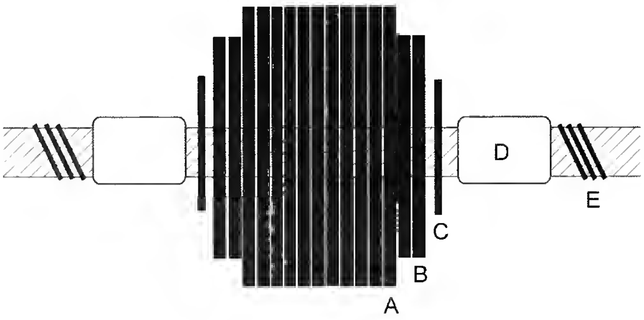

Figure 2

Schematic diagram of a cluster of disks (disk cluster) attached to trawl sweeps to raise the sweeps above the seafloor to test whether this gear modification reduces flatfish herding. Rubber disks (**A**, 20 cm-diameter, and **B**, 15 cm-diameter) were installed over the sweep cable, between clamps (**D**) that fix their location on the cable. Steel washers (**C**) prevented rubber disks from passing over clamps. Ropes seized over and tucked through cable (**E**) blocked clamps from shifting.

Catches from each trawl were kept separate throughout the sampling process. As catches entered the sampling area, they passed across a motion-compensated flow scale which provided a total catch weight. All individuals of four flatfish species (yellowfin sole, northern rock sole, flathead sole, and arrowtooth flounder) and two gadids (Pacific cod [*Gadus macrocephalus*] and Alaska pollock [*Theragra chalcogramma*]) were sorted into separate holding bins. These are the principal flatfish and gadid species harvested from the eastern Bering Sea shelf. Fish from each bin were then run across a second flow scale to measure the weight of each of these species. During the sorting of catch from each trawl, 50–150 fish of each species were sampled and their fork lengths were measured to 1-cm intervals to determine their size composition. These length samples were periodically taken from the catch as it passed through the sorting area to avoid bias in case fish size varied between parts of each catch. Because of their large size, limited holding space and handling requirements precluded adequate length sampling of Pacific cod.

Tows were planned to last 2 hours, unless catch sensors indicated substantial catches (>8 metric tons [t] per net) before that time. Actual tow durations ranged from 33 to 150 minutes. We eliminated hauls where debris (e.g., crab pots) was large enough to clog the net, or where gear components became entangled, because such conditions could influence gear performance and the size and composition of the resulting catch. Tow locations were selected in order to encounter commercial concentrations of the major flatfish species of the eastern Bering Sea shelf. Environmental parameters at the trawl, including depth, temperature and light level, were sampled throughout the experiment with a Mk9 logger (Wildlife Computers, Redmond, WA) mounted at the center of the trawl's headrope.

We used a high-resolution, rapid-update sonar (SoundMetrics DIDSON, Dual-frequency IDentification SONar, Lake Forest Park, WA) to observe how the sweep modifications affected seafloor contact. This was mounted in a protective sled, which was towed both behind the sweeps, to show interactions between the sweeps and the seafloor, and, separate from the trawl, across the track of a previous haul, to show marks left on the seafloor. These observations were made only on sweeps with the 20-cm disks. The sled was also towed across tracks from previous trawl tows with conventional and modified sweeps and was equipped with a video camera for detailed imagery.

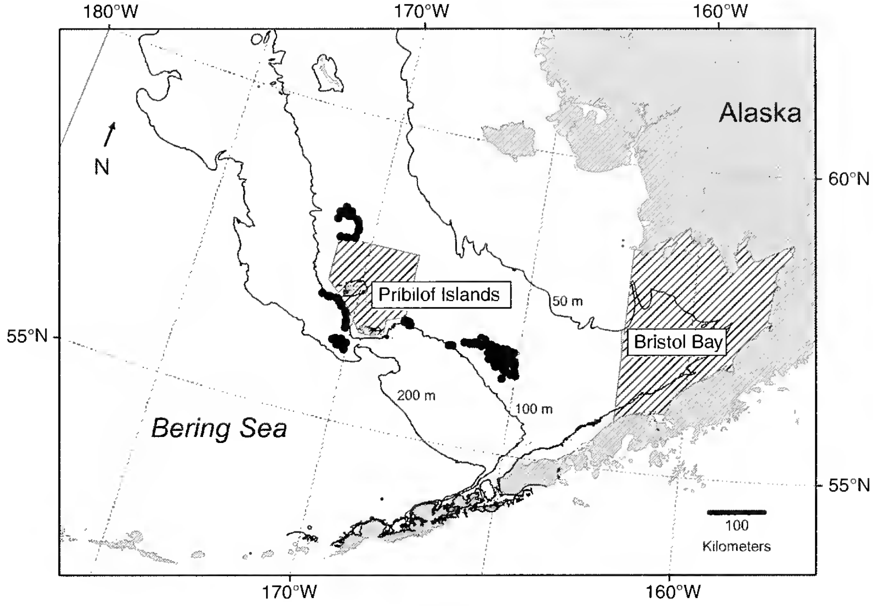

Figure 3

Fishing locations (●) in the eastern Bering Sea for the 2006 tests of the effects of raised sweeps on flatfish herding. Regions shaded with diagonal lines are areas of trawl closures around the Pribilof Islands and in Bristol Bay. Contour lines indicate depths.

To estimate the proportional change in catch due to the sweep modifications, the difference between the natural logarithms of the catch weights from modified and unmodified trawls (Log*Dif*) was calculated for each species from each twin-trawl haul:

$$\mathrm{Log}Dif = \ln(Catch_{modified}) - \ln(Catch_{unmodified}). \qquad (1)$$

This statistic, equivalent to the logarithm of the ratio between catches with modified and unmodified nets, was appropriate because absolute catch sizes were uncontrolled and varied widely. A statistic based on subtracting the untransformed trawl catches, like that for an ordinary paired t-test, would have varied proportionally to absolute catch rates, whereas catch ratios, as measured by Log*Dif*, were independent of the fish densities encountered during each tow. Averages and confidence intervals of Log*Dif* were computed for each species and sweep modification. To report these results as ratios, the averages and confidence intervals were then back-transformed with the exponential function. Catch results were only used for species with more than a minimal catch (>10 fish) in both nets. The null hypothesis that the sweep modifications did not affect catch was tested with a t-test of whether average Log*Dif* was different from 0, equivalent to a paired t-test for differences between the log-transformed catches.

To test whether the sweep modifications affected the size-selectivity for different fish species and to minimize variability, we pooled fish into three size classes for each species, except for arrowtooth flounder, where a wide size range made four size classes more appropriate. The size-class boundaries were set so that approximately one-third (one-fourth for arrowtooth flounder) of the fish in the combined control catches were in each category. To maintain consistency with the weight-based analysis of overall catch, and because the Alaska trawl fleet classifies fish sizes by weight, the boundaries of the size classes were defined by individual weights instead of lengths, and the catches of each size class were computed as weights, instead of numbers. Length-weight functions from the annual Bering Sea shelf trawl survey (NMFS, unpubl. data[1]) were used to convert the sampled lengths to their corresponding weights. The catch of each size class was estimated by expanding the proportion of that size class, by weight, from the sample of catch for that species. As with the total catch data, averages and confidence intervals were calculated. We used analysis of variance to test for differences between size classes for each combination of species and for each sweep modification.

Results

From 6 to 23 September 2006, 61 successful twin trawl hauls were conducted, including 19, 26, and 16 hauls with experimental sweep clearances of 5, 7.5, and 10 cm, respectively. Depths at these tow sites (Fig. 3) ranged from 70 to 117 m, and bottom temperatures ranged from 2.5° to 5.5°C.

Sonar imagery during towing showed that unmodified sweeps produced a continuous cloud of disturbed sediment due to contact with the seafloor. Variation in the density of that cloud appeared to result from contact with high and low spots on the seafloor, and rapid oscillation of strong and weak cloud intensity appeared to be due to vibration of the sweeps. In contrast, the sediment cloud from the modified sweep appeared only directly behind the disk cluster. The only clouds from the

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[1] NMFS, Alaska Fisheries Science Center, RACE Division, 7600 Sand Point Way NE, Seattle, WA

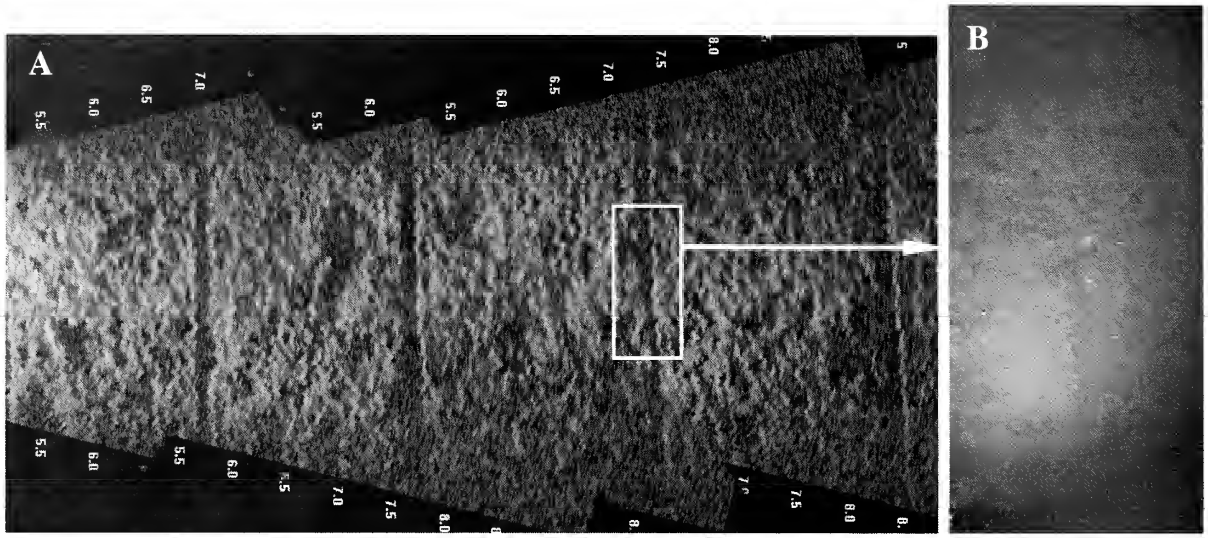

Figure 4

(**A**) Sonar and (**B**) video imagery of the seafloor after passage of the raised otter trawl sweeps. Video picture was taken as the seafloor sled passed over the location indicated on the sonar image. Otter trawl sweeps were raised with widely spaced disk clusters, which caused the parallel tracks seen in the sonar image and the flattened swath in the video image.

sweeps themselves were brief puffs after contact with high spots on the seafloor. Areas covered by the modified sweeps showed marks from the disk clusters that were approximately 10-cm wide separated by seafloor indistinguishable from unaffected areas (Fig. 4A). This disk cluster mark was approximately 5% of the 2-m interval between marks. This spacing is much shorter than the 9-m spacing on the cable because sweeps are sharply angled to their direction of movement (angle-of-attack). Images of such tracks from the video (Fig. 4B) showed a flattening of very low-profile surface textures.

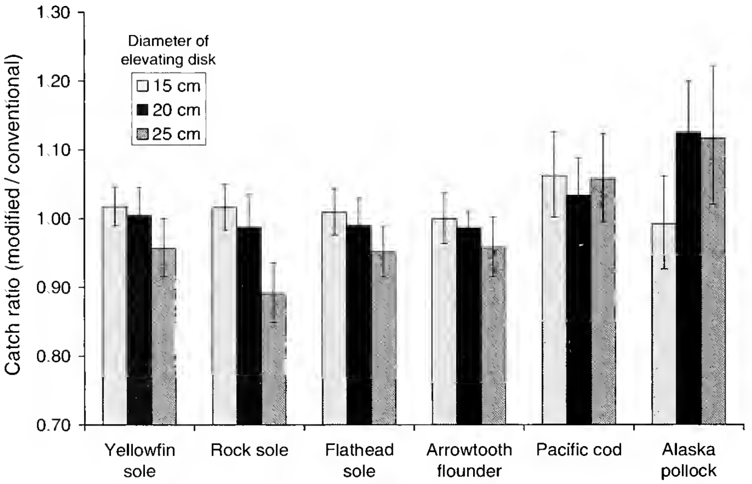

Figure 5

Estimates of and 95% confidence intervals for the ratios of fish catches with the modified trawl sweeps raised to three different heights off the seafloor to fish catches with conventional sweeps for the four principal flatfish species (yellowfin sole [*Limanda aspera*]; northern rock sole [*Lepidopsetta polyxystra*]; flathead sole [*Hippoglossoides elassodon*]; arrowtooth flounder [*Atheresthes stomias*]); and two principal gadid species: Pacific cod (*Gadus macrocephalus*); and Alaska pollock (*Theragra chalcogramma*) taken in Bering Sea trawl fisheries.

The use of 15-cm disks on the sweeps did not cause significant differences in catch rates (Log*Dif* was not different from 0) for any of the six species, and only the pollock catch rate changed (12% increase, $P=0.007$) with the 20-cm disks (Fig. 5). Northern rock sole and flathead sole catches both decreased significantly (–11%, $P<0.001$, and –5%, $P=0.02$, respectively) when the 25-cm disks were used, whereas pollock catch increased again (+12%, $P=0.03$). Decreases for the other two flatfish were also observed—although not statistically significant at the 0.05 level ($P=0.08$ for arrowtooth flounder and $P=0.07$ for yellowfin sole). A consistent decrease in the mean relative catch with increasing disk size for all of the flatfish species, although only significant for the largest disks, indicates that smaller effects may have occurred for the smaller disks that could not be statistically detected in our experiment. Pacific cod catches did not change significantly with any of the modifications.

For evaluating the likelihood of substantial losses of catch, the confidence intervals provide more information than the basic significance tests alone. For example, the lower confidence bounds for the effects of 20-cm disks on flatfish catches leave only a 2.5% (1 of 40) probability that catch losses would exceed 4–6%. Corresponding "worst case" losses for the 15-cm disks were even smaller. Similarly, although none of the Pacific cod catch results passed the threshold of a 95% two-tailed probability of being different from no change, all three of the confidence intervals were almost entirely above a value of 1. Therefore, a trawler could implement one of these modifications with little expectation of catching fewer Pacific cod and with a reasonable chance of slight increases in Pacific cod catch.

The size composition of each species from the unmodified nets (Fig. 6) showed truncation at the lower end of the size distribution, owing to use of large mesh in the body of the net (20 cm, stretch measure), intermediates (14 cm) and codends (15 cm) that release smaller fish. Although the proportions varied somewhat between experiments, each study encountered a representative range of sizes available to the commercial fishery.

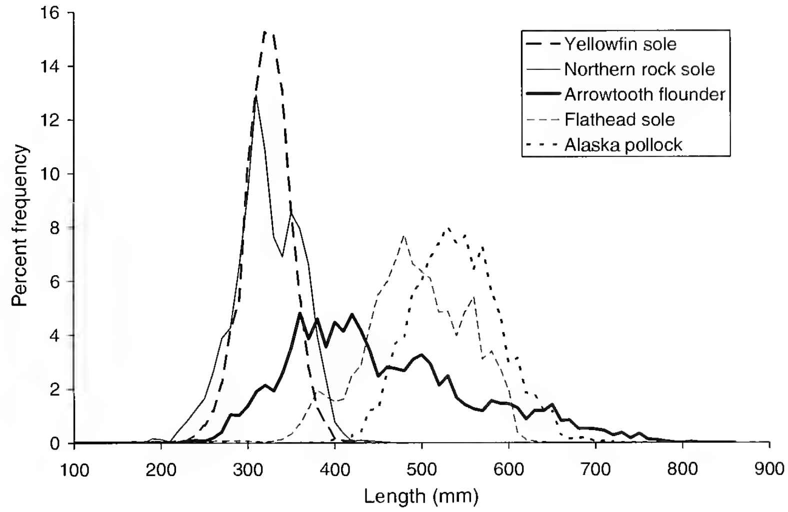

Figure 6

Size compositions for flatfish and gadid species taken during tests of whether raised trawl sweeps reduce herding of fish. Yellowfin sole (*Limanda aspera*); northern rock sole (*Lepidopsetta polyxystra*); flathead sole (*Hippoglossoides elassodon*); arrowtooth flounder (*Atheresthes stomias*); Pacific cod (*Gadus macrocephalus*); and Alaska pollock (*Theragra chalcogramma*).

ANOVA tests for differences in catch effects between major size classes (thirds or quartiles of control size frequencies) revealed no significant differences for any of the flatfish species (Fig. 7). One significant difference (P=0.04) was detected for pollock in sweeps with the smallest disks (15 cm), attributable to a lower catch rate of the smallest pollock. Confidence intervals were included in Figure 7 to aid comparisons between size groups within species and sweep modification classes. Confidence intervals were wider for the largest and smallest categories because few individuals from these ranges were encountered in some tows, increasing variability, whereas all tows had substantial numbers of fish in the central ranges.

Discussion

Flatfish can be effectively herded by trawl sweeps and with greatly reduced seafloor contact. Significant catch reductions, averaging 5% for flathead sole and 11% for rock sole, were only detected when 25-cm disks were installed that raised the sweeps 10 cm above the substrate at the ends of each 9-m section. No detectable catch reductions occurred during tests with smaller clearances (5 and 7.5 cm). Confidence intervals indicated only a 2.5% probability of catch reductions greater that 5% with 7.5-cm clearances. Nor did sweeps with such clearances appear to change size selectivity significantly.

Flatfish exhibit predator avoidance behaviors that allow them to be effectively herded by the sweeps. In contrast to roundfish, flatfish cease movement when a predator is detected and only flee upon very close approach (Ryer, 2008). Therefore, observed flatfish reactions to trawl gear (Main and Sangster, 1981; Rose, 1996; Ryer and Barnett, 2006) mostly occur at horizontal ranges of much less than 1 m. However, because conventional fishing gear has either continuous or closely spaced contact with the seafloor, there has been little or no information to assess the role of gear contact or proximity to the seafloor in either initiating or sustaining the flight behaviors that result in herding. Given the cryptic behaviors of flatfish, we could not assume that stimuli several centimeters above the seafloor would be as effective as those that would directly contact flatfish on the seafloor. The current results demonstrate that flatfish do respond with effective herding behaviors to sweep cables displaced from the seafloor by 5 to 10 cm. Even the largest of the flatfish encountered here would not have contacted the raised sweeps if they remained resting on the seafloor. At the highest clearance (10 cm), slightly reduced catches indicated that the flight response began to break down and some of the flatfish were not herded as well as with the conventional sweeps. Winger et al. (2004) found that flatfish size

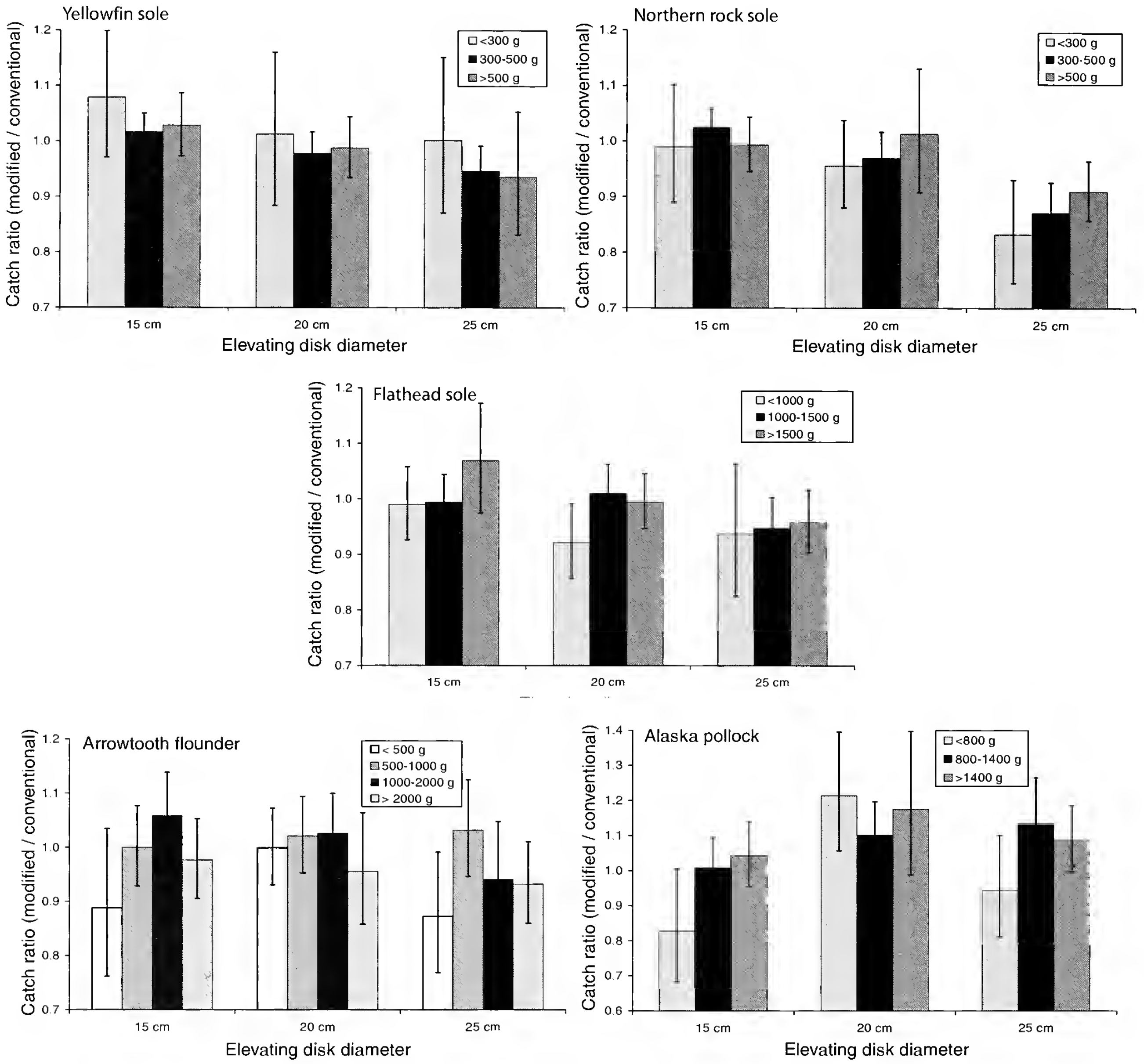

Figure 7

Estimates of and 95% confidence intervals for ratios of fish catches during tests with modified trawl sweeps raised to three different heights off of the seafloor to catches with conventional sweeps for broad size classes of four principal flatfish species and a principal gadid species taken in Bering Sea trawl fisheries: yellowfin sole (*Limanda aspera*); northern rock sole (*Lepidopsetta polyxystra*); flathead sole (*Hippoglossoides elassodon*); arrowtooth flounder (*Atheresthes stomias*); and Alaska pollock (*Theragra chalcogramma*).

affected behavioral responses to approaching sweeps, including tailbeat frequency and swimming endurance. Although any of these behaviors could affect herding-related capture rates, the current study did not indicate behavioral differences between size classes in response to the elevated sweeps.

We followed commercial practices in the gear type used, weight-based catch metrics, towing durations, catch handling, and round-the-clock operations. This procedure was undertaken to increase the relevance of our results to those with the greatest stake in deciding on the use of these modifications: the fishermen and fishing companies. Fishermen actively participated in designing the gear modifications and in conducting the research.

To examine consequences of using modified sweeps in the fishery and to improve precision, all tows were analyzed together, including day and night tows, even though light levels affect the herding process (Ryer and Barnett, 2006). The effects of light on flatfish herding are analyzed and reported in a separate paper (Ryer et al., 2010).

Although not the focus of this study, an unexpected result was the increase in pollock catches that occurred with two of the sweep modifications. Pollock herd differently from flatfish, reacting to stimuli at much greater distances (Rose, 1996). The forward sections of the most modern pollock trawls have "meshes" that are more than 25-m long. Although large groups of pollock could easily swim through such meshes, they still avoid the netting and are eventually herded into parts of the net that physically restrain them. These nets would not work if pollock herded only at short ranges. Separation of the sweeps from the seafloor, or the disk clusters themselves, could have increased visibility of the sweeps, which may have enhanced pollock herding. Both factors would be reduced at the smallest disks, where herding improvement was not detected.

Sonar observations of the elevated sweeps showed that their interaction with the seafloor was radically changed. The continuous sediment clouds produced along the entire length of the unmodified sweeps were, for the modified sweeps, reduced to isolated clouds behind each disk, indicating substantial reductions in the area of direct contact. Therefore, any effects based on direct contact, as well as resuspension of sediments, should have been greatly reduced. The sonar images of the seafloor after passage of the sweep showed that the contact area of the disks was approximately 5% of the total swept area. Seafloor texture between the disk tracks was indistinguishable from unaffected areas, but areas covered by conventional sweeps showed slight smoothing. The seafloor directly contacted by the disks was uniformly smoothed. Although the texture change due to conventional sweeps appeared slight, the resuspension observed during fishing indicated some disturbance of the bottom and we believe that the substantial reduction of contact due to using the disks more than compensates for any increased disturbance to the small area directly under the disks.

In another recent study (Guyonnet et al., 2008), the concept of slightly raising trawl sweeps, therein called "legs," was also applied to reduce their impact on the seafloor. Instead of disk clusters, Guyonnet et al. used neutrally buoyant sweep material that was weighted only by dangling chains attached every 50 cm. They also found no significant effects on catch composition or size selectivity for target animals. They found that damage to benthic animals was reduced with the alternative gear.

Our results alone, although promising, do not address the full potential of sweep modifications to reduce the effects on the seafloor of trawling for Bering Sea flatfish. Although creating several centimeters of separation between the sweeps and the seafloor greatly reduces the potential for damage to infauna and small epifauna, it does not prevent contact with seafloor features and animals larger than that spacing. The vulnerability of ecosystem features to trawling operations is a function of the amount of damage caused by each trawl exposure (e.g., the proportion of a particular species in the path of a trawl that dies due to trawl contact) and the frequency and coverage of the trawling effort. An analysis of such factors for the Bering Sea shelf highlighted structure-forming animals as the seafloor feature most vulnerable to trawling.[2] The structure-forming animals of the eastern Bering Sea shelf are generally small and flexible; therefore it is quite conceivable that creating a space below the sweeps could also reduce damage to these animals. That potential is being examined by the authors in a subsequent study that will focus on how these sweep modifications change damage rates to structure-forming animals of the Bering Sea shelf.

Successful gear modifications for reducing trawling effects on seafloor habitats would add a habitat protection option in addition to area closures and gear switching. Closures of areas to trawling can move fishing effort from productive grounds, and therefore can increase the total effort required or concentrate fishing and its effects in the remaining fishing grounds (Fujioka, 2006). The list of alternative gear for harvesting these flatfish is quite limited and none are without some negative effects on habitat. With beam trawling, herding sweeps are not used to concentrate fish into the path of the capture device. Therefore, the entire area from which fish are collected is swept with the capture net itself. Studies to reduce the effects of beam trawls on habitat have focused on other stimuli to move fish from the seafloor into the net (van Marlen et al., 2005). The capture process for demersal seines is similar in many ways to that of Alaska otter trawls with long sweeps—weighted cables are pulled across the seafloor to herd fish into the path of a capture net. Demersal entangling nets depend on natural movements of the fish to bring them to the gear, and therefore they are effective only during periods when fish are actively moving. They are still unlikely to produce catch rates similar to those produced with trawls unless vast fleets of nets are deployed. Such extensive net deployments would exacerbate the most notable problem with demersal entangling nets—ghost fishing of derelict and lost gear. Finally, although longline fishing is the foundation for one of the most successful commercial flatfish fisheries (Pacific halibut), most flatfish species are not of the size and do not have a predatory diet that make longlines particularly effective.

Implementing the trawl gear modifications described here would require some adaptations in equipment and handling methods for fishermen. The volume of the elevating devices would require additional space on deployment reels or net drums, thus requiring either that sweep lengths be shortened to fit onto the reels or larger reels be installed on vessels. The disks would

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[2] Final environmental impact statement for essential fish habitat identification and conservation in Alaska. April 2005 [online]. http://www.fakr.noaa.gov/habitat/seis/efheis.htm.

also complicate deployment and retrieval because they do not wrap as evenly onto reels as unmodified sweeps. Potential advantages with the use of disks would include longer usability of sweeps and reduced drag (improved fuel efficiency), both due to reduced contact of the sweeps with the seafloor. An important factor in identifying these implementation and operational issues early, as well as in the development of potential solutions, has been the direct participation of the fishing industry in this research and our ability to conduct these tests under conditions identical to most of the important operational aspects of the commercial fishery.

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Flatfish herding behavior in response to trawl sweeps: a comparison of diel responses to conventional sweeps and elevated sweeps

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Abstract—Commercial bottom trawls often have sweeps to herd fish into the net. Elevation of the sweeps off the seafloor may reduce seafloor disturbance, but also reduce herding effectiveness. In both field and laboratory experiments, we examined the behavior of flatfish in response to sweeps. We tested the hypotheses that 1) sweeps are more effective at herding flatfish during the day than at night, when fish are unable to see approaching gear, and that 2) elevation of sweeps off the seafloor reduces herding during the day, but not at night. In sea trials, day catches were greater than night catches for four out of six flatfish species examined. The elevation of sweeps 10 cm significantly decreased catches during the day, but not at night. Laboratory experiments revealed northern rock sole (*Lepidopsetta polyxystra*) and Pacific halibut (*Hippoglossus stenolepis*) were more likely to be herded by the sweep in the light, whereas in the dark they tended to pass under or over the sweep. In the light, elevation of the sweep reduced herding, and more fish passed under the sweep. In contrast, in the dark, sweep elevation had little effect upon the number of fish that exhibited herding behavior. The results of both field and laboratory experiments were consistent with the premise that vision is the principle sensory input that controls fish behavior and orientation to trawl gear, and gear performance will differ between conditions where flatfish can see, in contrast to where they cannot see, the approaching gear.

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Trawl catches for many fish species exhibit diel patterns (Casey and Myers, 1998). This is generally viewed as a product of two independent factors: availability and catchability of the fish species. Many gadids exhibit diel changes in availability associated with vertical migration (Beamish, 1965; Casey and Myers, 1998; Schabetsberger et al., 2000). Gadids aggregate close to the bottom during the day and are highly available to bottom trawls. At night, dispersal into the overlying water renders them less available. Interestingly, for many flatfish species the opposite pattern, higher catches at night, has been observed (Walsh, 1991; Walsh and Hickey, 1993; Casey and Myers, 1998). Seasonal migrations will occasionally take flatfish into the water column (Metcalfe et al., 1990; Nichol and Sommerton, 2009), as will the occasional exploitation of pelagic prey. However, under normal circumstances many flatfish species appear to remain on the bottom and are consistently available to trawl gear, day or night. As a consequence, greater flatfish catches at night are thought to be associated with higher catchability, that is, with a decreased ability to evade capture (Ryer, 2008).

Video cameras mounted on trawls, as well as supplemental bag nets behind the main net, have documented extensive flatfish escapement beneath the footrope during the day (Main and Sangster, 1981; Walsh, 1988). For obvious technical reasons, behavior in front of the footrope, or sweeps, at night has not been observed in field studies, except with flash photography (Walsh and Hickey, 1993). However, laboratory experiments indicate that northern rock sole (*Lepidopsetta polyxystra*), Pacific halibut (*Hippoglossus stenolepis*), and English sole (*Parophrys vetulus*) are more likely to rise or hop into the water column during darkness, than to herd (Ryer and Barnett, 2006). By moving off the bottom, these fish remove themselves from the "zone of influence" of the ground gear, and as they cease swimming they pass over the footrope and into the net. This behavior potentially explains why flatfish are captured in greater numbers at night.

This paradigm, i.e., higher flatfish catches at night, stems largely from a series of published studies (Main and Sangster, 1981; Walsh, 1988, 1991; Walsh and Hickey, 1993; Casey and Myers, 1998; and references therein), based on survey trawls. On survey trawls, the combined length of bridles and sweeps is typically minimized. In contrast, on commercial flatfish trawls lengthy sweeps are used to herd fish inward toward the net (Winger et al., 1999, 2004). On some modern flatfish trawls these sweeps may be up to 400 m in length, and as much as 90% of the seafloor is subject to the action of gear which is designed to affect capture by manipulating flatfish swimming behavior. But for the very reason that footropes are more efficient in the dark, sweeps may be less efficient. If flatfish, unable to see the approaching sweep, rise or hop into the water column, rather than herding as happens during the day, they will pass over the sweep and be lost to the catch. This situation raises the possibility that flatfish trawls that rely upon sweep herding may capture more flatfish during the day than during the night—a pattern not seen with survey trawls, which have minimal sweeps.

In this study we investigated the performance of trawls equipped with sweeps under day and night conditions, using a combination of manipulative at-sea and laboratory procedures. For our at-sea experiment, we used a data set acquired during a series of cruises in the eastern Bering Sea, the goal of which was to evaluate sweeps designed to reduce damage to benthic habitat (Rose et al., 2010). In brief, trawling was conducted with sweeps that were elevated, to various degrees, off the seafloor to evaluate the trade-off between reductions in habitat disturbance and decreased flatfish herding efficiency. Here we test hypotheses related to our principle premise: flatfish behavior initiated by ground-gear is principally controlled by ambient light levels. More specifically, first we test the hypothesis that trawls configured with control (commercial type) sweeps in contact with the bottom, will catch more flatfish during the day than during the night. Following from this, we test a second related hypothesis: the elevation of sweeps off the bottom will have differential effects, day as opposed to night. During the day, elevation will reduce sweep efficiency, resulting in lower flatfish catch. During the night, because sweeps are already relatively ineffective, elevation of the sweeps will have no influence upon their efficiency, as reflected by flatfish catch. Lastly, we conducted comparable experiments under both light and dark conditions, using simulated ground-gear in the laboratory where behavior could be quantified, to ascertain whether the proposed effects of elevated sweeps on catch are directly attributable to ambient-light–mediated differences in flatfish behavior in relation to ground gear.

Methods

At-sea experiments

Tows of paired trawls (control and elevated sweeps) were conducted during September 2007 in the eastern Bering Sea onboard the FV *Cape Horn*. Details of gear and onboard procedures can be found in Rose et al. (2010). Briefly, the Cape Horn is a 47-m trawler processor, configured so as to allow twin trawling, i.e., fishing with two identical nets side-by-side. Each net had a set of independent 180-m sweeps, being spread by one otter board on each side of the vessel, and connected in the middle by a towed weight (clump). The sweeps were composed of 5-cm diameter combination rope, constructed of steel cable and covered by polyethylene fiber. Modifying the sweeps on one net, while keeping all other trawl characteristics consistent, allowed the difference between the two catches to reflect the effect of the modification. In this field study, disk clusters were attached to the experimental sweeps at 9-m intervals. The disks were either 15, 20, or 25 cm in diameter. This created a nominal spacing between the sweeps and the seafloor of 5, 7.5, and 10 cm, respectively. Test tows were made with modified sweeps on one net and unmodified sweeps on the other. Halfway through each experiment, the modified sweeps and unmodified sweeps were switched (left to right, right to left).

Catches from each trawl were kept separate until the entire catch had been sampled. As catches entered the sampling area, they were passed across a motion-compensated flow scale to determine total catch weight. The five or six most abundant species were then completely sorted into holding bins. Fish from each bin were then run across a second flow scale to measure the weight of each of those species. To estimate the weight of other species, samples of the unsorted catch were taken at intervals, sorted, and weighed by species. The composition of these samples was then expanded to the weight of the entire catch by calculating the fraction of the sample weight to the total catch weight. For the species cited in this paper, Pacific halibut and Alaska plaice catches were estimated from the samples and all other species were fully weighed on the second flow scale. During the sorting phase, samples of 50–150 fish of each species were drawn and measured to determine their length composition. Length samples were taken from throughout the catch as it passed through the sorting area and the length of each individual in the sample was measured

Sixty-one paired hauls were made over depths ranging from 70 to 117 m. Ambient light on the bottom is greatly influenced by water depth. To minimize potential depth effects upon ambient light, we limited our analysis to hauls where depth was between 79 and 94 m: a 15-m range. In addition, we eliminated hauls where large debris (crab pots, etc.) were encountered, or where gear components became entangled, assuming that such conditions would influence gear performance and catch. After examining *in situ* light measurements (Wildlife Computers, MK9 light meter, Redmond, WA) we further eliminated daytime hauls where light levels fell below 1.0×10^{-4} µmol photons/m^2/s, and nighttime hauls exceeding 1.0×10^{-5} µmol photons/m^2/s. This step eliminated hauls made around dusk or dawn and set a clear differentiation between daytime and nighttime light. In the resulting data set (36 hauls), mean tow depth did not differ between nighttime and daytime tows (day: n=7, mean [$\bar{x}$]=82 m, standard error [SE]=1; night: n =19, $\bar{x}$=84 m, SE=1; $t_{[34]}$=1.54, P=0.133). Tow durations ranged from 33 to 150 min, being somewhat longer at night ($\bar{x}$=115.8, SE=5.9) than during the day

($\bar{x}$= 87.5, SE=6.3, $t_{[34]}$=3.28, P = 0.003). During long tows, accumulating catch can distort meshes and back up into the intermediate portion of the net, altering gear selectivity (Herrmann, 2005). However, catches in this study were small compared to net capacity, never filling the codend. Hence, we assume that differences in duration between day and night did not influence net performance or fish catchability in a manner that would bias our results. Similarly, during long tows proportionately more fish will tire and fall back into the net, particularly so for many roundfish species, which can swim for prolonged periods in front of the net (Main and Sangster, 1981). However, flatfish typically swim for less than 1 minute in front of nets (Ryer, 2008), and thus this source of bias was also unlikely in our study.

For our first analysis, we compared daytime and nighttime catches from the control nets only; where sweeps were in contact with the bottom along their entire length. Catch per unit of effort (CPUE: kg/min) was calculated for total catch (all species) as well as for six flatfish species: yellowfish sole (*Limanda aspera*); flathead sole (*Hippoglossoides elassodon*); arrowtooth flounder (*Atheresthes stomias*); rock sole (*Lepidopsetta* spp.); Alaska plaice (*Pleuronectes quadrituberculatus*); and Pacific halibut. CPUE values were natural log (ln) transformed and tested for day and night differences with *t*-tests (Sokal and Rohlf, 1969). Where variances were heteroscedastic, Satterthwaite's adjusted degrees of freedom were used (Snedecor and Cochran, 1980). Because CPUE was based upon weight, we also compared mean total length between daytime and nighttime hauls for each flatfish species.

For our second analysis, we used the subset of samples from trawls where 25.4-cm disks were attached to elevate sweeps of the experimental net to an approximate height of 10 cm (the distance between sediment surface and bottom of the sweep material). For this analysis, catch of the experimental net was compared to that of the paired control net (with bottom contact sweeps) by using a paired *t*-test (Sokal and Rohlf, 1969). Separate analyses were conducted for daytime (n=10 pairs) and nighttime (n=5 pairs) hauls. Similar analysis was conducted for flatfish lengths.

Laboratory experiments

Northern rock sole and Pacific halibut were collected as age-0 juveniles by using a 2-m plumb-staff beam trawl from Chiniak Bay, Kodiak, Alaska. Fish were transported to the Hatfield Marine Science Center in Oregon and reared in 2.2-m (diameter) circular tanks with flow-through seawater (28–35‰, 9°C [± 1°]) on a diet of krill and gelatinized food. After reaching age 1, fish were transferred to 3-m diameter pools for continued growth.

Simulated sweep exposure took place in an elongated tank (10.7×1.5×1.2 m) filled to a depth of 0.9 m. This tank was provided with flow-through seawater (28–35‰) and located in a light-proof room, allowing for control of illumination by an overhead bank of fluorescent lamps. The tank bottom was covered to a depth of 4 cm with sand, allowing flatfish to completely bury themselves. Details of this apparatus are presented elsewhere (Ryer and Barnett, 2006) and will only be described briefly here. By means of a moveable carriage a simulated sweep was propelled down the length of the tank. This sweep consisted of a piece of 5-cm diameter PVC pipe, painted green to resemble the actual sweep used in the field study. It could be positioned so that it ran down the tank in contact with the bottom, or elevated so that it was approximately 10 cm off the bottom.

Fish were maintained on a 12/12 h photo period during all experiments, with lights turned on at 0700 and off at 1900. At 1600 on the day before the trials, the length of the tank was subdivided into three equal 3-m sections, by means of four removable partitions, of which two of these partitions prevented fish from moving to the extreme ends of the tank. Next, fish were introduced to each of the three main sections of the tank. This sectioning assured that fish would not aggregate in a single area of the tank. At 0800 on the day of trials, the footrope carriage was lowered into the tank, behind one of the end partitions and secured to its tracks. Then the lighting was either turned off (dark trials) or kept on (light trials), and fish were allowed 2 h acclimation before a trial. Illumination at the sand surface was measured once at the beginning of the study. For light trials, illumination was approximately 1.5 µmol photons/m^2/s (~125 lux), whereas, for dark trials illumination was <1×10^{-8} μmol photons/m^2/s (~10^{-6} lux). Both species used in this study have the same light thresholds (10^{-5} μmol photons/m^2/s) for visual discrimination of small motile prey (Hurst et al., 2007), and we assumed they would see approaching footrope in the light trials, but not in the dark trials. Illumination was measured with a research radiometer (International Light Inc., Model IL1700, Peabody, MA) equipped with a 2π PAR (photosynthetically active radiation) sensor. Water supply to the tank was filtered through sand, making it unlikely that water clarity, and hence light levels, changed appreciably from day to day. At 1000 h, immediately before a trial, the partitions were removed; for dark trials red flashlights were used during this process, and care was taken to avoid shining the lights directly into the tank. Five minutes later the footrope carriage was pulled from one end of the tank to the other at a speed of 1.0 m/s (± 0.1 m/s), a speed roughly equal 3.6 km/h or 2 knots; flatfish trawls are commonly towed at 2–5 knots. Afterwards, the lights in the room, if turned off, were turned back on and rakes were used to herd fish back into each of the three main sections of the tank, after which the partitions were put back in place and the footrope carriage was removed from the tank. This entire process was repeated in the afternoon, using the opposite lighting from that of the morning: at 1200 h, a footrope carriage was lowered into the tank and lighting was adjusted; at 1400 h, partitions were removed and the footrope carriage was pulled. We assume that this alternation in treatment order precluded any bias attributable to flatfish habituation or learning.

Positioned behind and above the footrope were three (50W) infrared LED (light emitting diode) lamps, aimed forward and down, so that they illuminated the footrope and tank bottom immediately in front of the footrope. The wavelength of light emitted by these lamps peaked at 880 nm, and emissions dropped to 0 below 760 nm. Most fish are insensitive to light at those wavelengths (Douglas and Hawryshyn, 1990) and results from light-threshold feeding studies for all three flatfish species used in this study are consistent with this generalization (Hurst et al., 2007). Two underwater video cameras (Aqua-Vu, model ZT-120, Crosslake, MN) were mounted alongside the lamps, also directed at the area in front of the footrope. This arrangement allowed for visual monitoring out to 1.1 m in advance of the footrope. The video footage was captured from a remote location by digital mini-DV recorders.

Trials were conducted with three age classes of Pacific halibut: age-1, age-2, and age-3, as well as age-2 northern rock sole. For age-3 Pacific halibut, three groups of five fish each were examined. Trials took place over two consecutive days. On the first day sweep height was randomly set to either the "in contact" or "elevated" position. On the second day the alternative position was used. During each day, fish were exposed to the simulated sweep approach twice; once in the light and once in the dark. The order of application of light vs. dark trials was also randomly determined. After the second day fish were then removed from the tank, their total length was measured, and they were replaced by a new group. Age-3 Pacific halibut ranged from 37–52 cm in total length.

For age-2 Pacific halibut, age-1 Pacific halibut, and age-2 rock sole, groups consisting of 10 fish each were trialed differently. Each group was trialed for only a single day, at one sweep height. For age-2 Pacific halibut, six groups were trialed at each sweep height. For age-1 Pacific halibut and age-2 northern rock sole, five groups were trialed at each sweep height. As before, the order of light and dark trials was randomized. Age-2 Pacific halibut ranged from 19–31 cm, age-1 halibut from 8–14 cm, and age-2 northern rock sole from 9–17 cm.

Fish behavior was quantified by using the slow-motion playback of digital video. First, the number of fish encountered, i.e., observed, as the sweep made its transit from one end of the tank to the other, was recorded from each trial. Then the initial behavioral response of each observed fish was assigned to one of four categories: 1) pass under, 2) hop, 3) rise, and 4) herd. Fish characterized by "under" either did not react at all to the approaching sweep, or reacted when contacted by the sweep, but passed under the sweep as it progressed down the tank. "Hop" characterized fish that reacted to the sweep with one or two sinusoidal body undulations, typically after being struck by the sweep, which resulted in the fish "hopping" off the substrate. However, this initial startle reaction was not followed by any further swimming, such that the fish tended to hang stationary in the water, and passed over the sweep as it progressed down the tank. "Rise" characterized the motion of fish that departed the bottom with sustained swimming in an upward direction, such that the distance between fish and bottom continuously increased as the fish swam. This was in contrast to fish characterized by "herd" where fish maintained a distance of less than one body length between themselves and the bottom as they swam along in front of the sweep, i.e. herding behavior. Ryer and Barnett (2006) investigated whether initial orientation, i.e., the direction fish were facing, influenced behavioral response. No relationship was observed, and consequently, no data on fish orientation were recorded in this study. Categorical data on behavioral response were pooled across replicate groups and analyzed by contingency table analysis by using log-linear models (Fienberg, 1980).

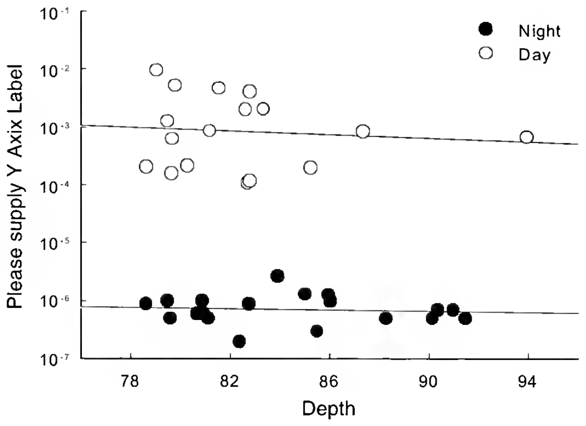

Figure 1

In situ natural log-transformed light data for trawl tows conducted during day and night, plotted by mean depth over the course of each tow. Regression analysis indicated no effect of depth upon ambient light over this relatively narrow range of depths and hence, regressions are plotted as zero-slope lines.

Results

At-sea experiment

Mean ambient light on the seafloor (Fig. 1) was greater during daytime tows (2.0×10^{-3} µmol photons/m^2/s) than during nighttime tows (8.4×10^{-7} µmol photons/m^2/s, $F_{[1,33]}=352.76$, $P<0.001$). However, over the relatively narrow range of tow depths used in this analysis, depth had no influence upon bottom ambient light level ($F_{[1,33]}=0.27$, $P=0.607$). Mean total catch (CPUE) in terms of weight (kg/min) was greater during the day than at night (Table 1, day: $\bar{x}=100.6$ kg, SE=9.61; night: $\bar{x}=53.07$ kg, SE=6.14). This pattern of diurnally

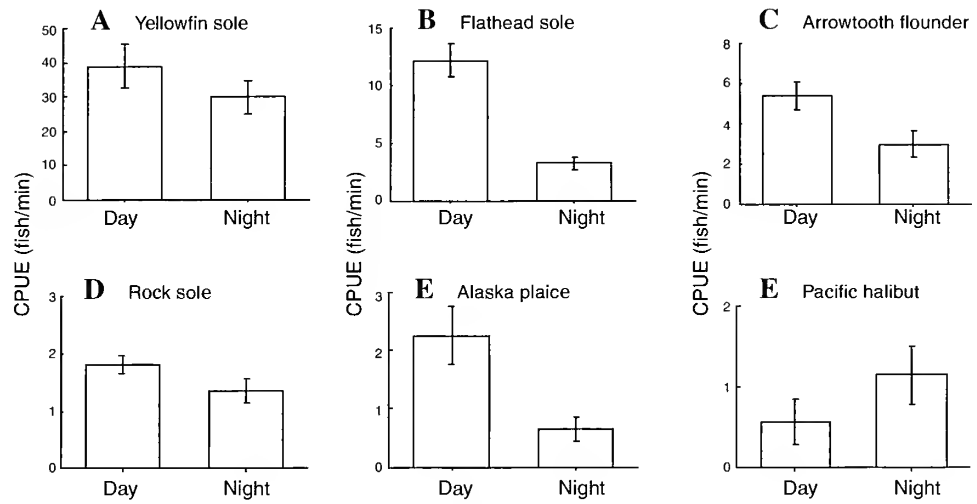

Figure 2

Mean catch per unit of effort (CPUE) ±1 standard error (SE) for daytime and nighttime hauls for each of six flatfish species from control nets where the sweep was in contact with the seafloor: (**A**) yellowfin sole (*Limanda aspera*); (**B**) flathead sole (*Hippoglossoides elassodon*); (**C**) arrowtooth flounder (*Atheresthes stomias*); (**D**) rock sole (*Lepidopsetta* spp.); (**E**) Alaska plaice (*Pleuronectes quadrituberculatus*); and (**F**) Pacific halibut (*Hippoglossus stenolepis*).

Table 1

Statistics for a comparison of day and night trawl catches, by total catch, and catch of six individual species of flatfish. For both day and night tows, trawl nets were equipped with control sweeps (that had contact with the bottom). Where needed, Satterthwaite's adjusted degrees of freedom were used to mitigate for nonhomogeneity of variance.

Species	*t*-test statistic	df	*P* value
Total catch	4.85	31.3	<0.001
Yellowfin sole (*Limanda aspera*)	1.71	30.6	0.097
Flathead sole (*Hippoglossoides elassodon*)	−7.44	34	<0.001
Arrowtooth flounder (*Atheresthes stomias*)	−3.26	34	0.003
Rock sole (*Lepidopsetta* spp.)	−2.38	29.3	0.024
Alaska plaice (*Pleuronectes quadrituberculatus*)	−3.74	26.4	0.001
Pacific halibut (*Hippoglossus stenolepis*)	1.58	34	0.126

larger catches was also exhibited by four out of six flatfish species examined (Table 1, Fig. 2). Flathead sole, arrowtooth flounder, rock sole, and Alaska plaice were all characterized by higher CPUE during the day. Yellowfin sole and Pacific halibut exhibited no significant differences in catch between day and night. Of the four species for which fish total length was measured in catch subsamples (i.e., yellowfin sole, flathead sole, arrowtooth flounder, and rock sole), fish tended to be slightly larger at night. This was only statistically significant for yellowfin sole ($t_{[24.4]}$=3.93, P=0.001), where fish averaged 1 cm longer during the night ($\bar{x}$=32.8 cm, SE=0.2) than during the day ($\bar{x}$=31.8 cm, SE=0.1), and rock sole ($t_{[32]}$=2.91, P=0.006), where fish averaged 0.9 cm longer during the night ($\bar{x}$=33.3 cm, SE=0.2) than during the day ($\bar{x}$=32.4 cm, SE=0.2).

The effect of elevating sweeps 10 cm off the bottom differed, depending upon whether tows were made during the day or night (Fig. 3). During the day, total catch tended to decrease when sweeps were elevated (Table 2, elevated: $\bar{x}$=93.4, SE=8.7; control: $\bar{x}$=100.6, SE=9.6). However, during the night, elevation of sweeps had little influence upon catch (elevated: $\bar{x}$=55.1, SE=6.8; control: $\bar{x}$=53.1, SE=6.1). This same pattern was evident for four out of six flatfish species examined. Species for which daytime elevation of sweeps decreased catch included flathead sole, arrowtooth flounder, rock sole, and Alaska plaice. Sweep configuration had no significant effect on

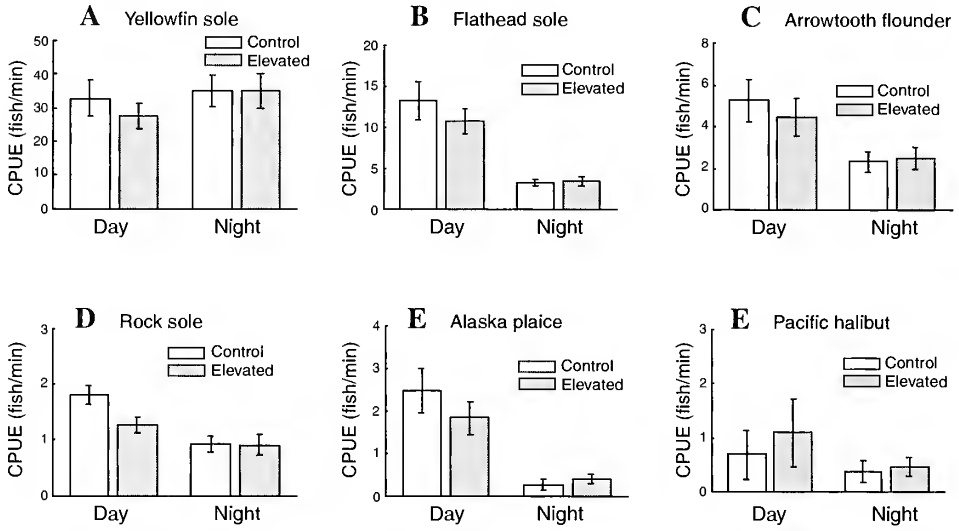

Figure 3

Mean catch per unit of effort (CPUE) ±1 standard error (SE) for daytime and nighttime catches of each of six flatfish species from both control nets, where the sweep was in contact with the seafloor, as well as experimental nets where the sweep was elevated 10.2 cm off the seafloor: (**A**) yellowfin sole (*Limanda aspera*); (**B**) flathead sole (*Hippoglossoides elassodon*); (**C**) arrowtooth flounder (*Atheresthes stomias*); (**D**) rock sole (*Lepidopsetta* spp.); (**E**) Alaska plaice (*Pleuronectes quadrituberculatus*); and (**F**) Pacific halibut (*Hippoglossus stenolepis*).

Table 2

Statistics for comparison of total catch and catch of six individual species of flatfish between trawl nets equipped with control (bottom contact) and those equipped with elevated (10 cm off bottom) sweeps, from both day and night tows.

Species		Paired *t*-test statistic	df	*P* value
Total catch	Day	2.11	9	0.064
	Night	−0.22	4	0.834
Yellowfin sole (*Limanda aspera*)	Day	1.84	9	0.099
	Night	0.09	4	0.935
Flathead sole (*Hippoglossoides elassodon*)	Day	2.33	9	0.045
	Night	−0.78	4	0.481
Arrowtooth flounder (*Atheresthes stomias*)	Day	4.35	9	0.002
	Night	−0.71	4	0.519
Rock sole (*Lepidopsetta* spp.)	Day	5.42	9	<0.001
	Night	0.23	4	0.830
Alaska plaice (*Pleuronectes quadrituberculatus*)	Day	2.39	9	0.041
	Night	−0.67	4	0.539
Pacific halibut (*Hippoglossus stenolepis*)	Day	−0.59	9	0.753
	Night	0.29	4	0.785

daytime catches of yellowfin sole or Pacific halibut. In contrast to daytime results, elevated sweeps had no effect upon nighttime catches for any species. Of the four species that were measured, fish lengths did not differ between tows with elevated sweeps and control tows, regardless of time of day ($P>0.05$ for each species, day and night).

Laboratory experiment

Overall, 28% of fish initiated herding behavior in response to simulated sweep disturbance. Herding was most prevalent in the light, and tended to be replaced by fish passing under the sweep, as well as hopping or rising off the bottom in the dark (Fig. 4). There was also

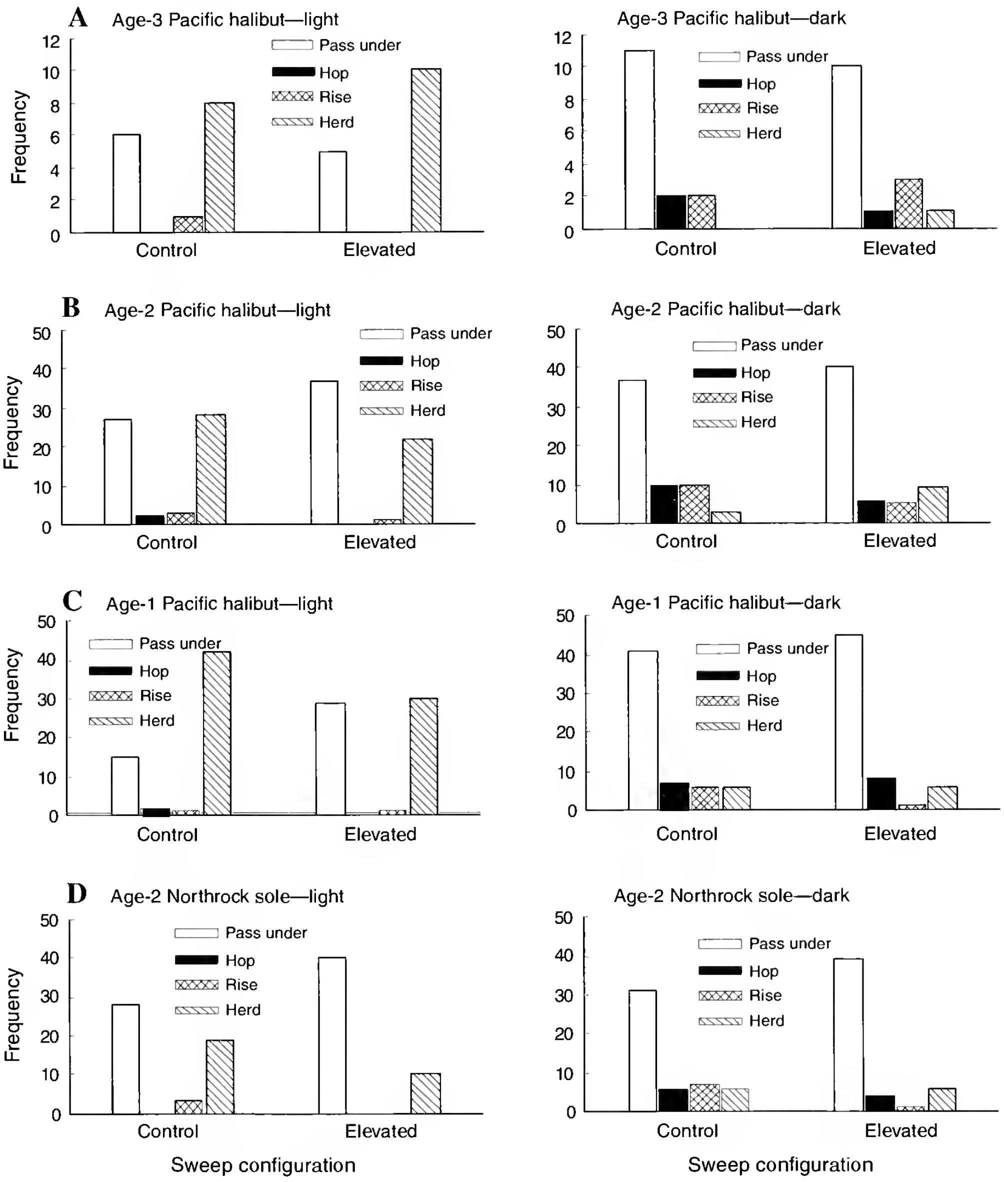

Figure 4

Behavioral response of flatfish, under light and dark conditions, with the simulated sweep both in contact (control) and elevated 10 cm off the bottom: (**A**) age-3 Pacific halibut (*Hippoglossus stenolepis*); (**B**) age-2 Pacific halibut; (**C**) age-1 Pacific halibut; and (**D**) age-2 northern rock sole (*Lepidopsetta polyxystra*). "Pass under" represents fish that either did not react to the sweep, or reacted late, such that they passed under the sweep as it progressed down the tank. "Hop" characterized fish that reacted to the sweep with one or two body undulations, but almost immediately pass over the sweep. "Rise" characterized fish in which the initial jump off the bottom was followed by sustained swimming in an upward direction, such that the distance between fish and bottom continuously increased as the fish swam. "Herd" characterized fish which, after reacting to the gear, swam along in front of the sweep, close to the bottom, typically maintaining a distance of less than one body length between themselves and the bottom.

a tendency for herding in the light to decrease when the sweep was elevated. These observations are supported by results of log-linear model analysis, in which ambient light (light, dark) mediated the influence of sweep height upon behavioral response ($G_{[3]}$=9.96, P=0.019). All three age classes of Pacific halibut, and northern rock sole, behaved comparably; there were no significant effects of species or age on the type of response displayed, or interactions with light level or sweep height ($P>0.05$ for all). Examination of Figure 4 could lead one to conclude that age-3 halibut behaved somewhat differently than the other species and age groups. However, the number of age-3 halibut tested ($n=15$) was small compared to each of the other species and age groups ($n>50$ for each), and as a consequence, had little influence upon our statistical model. We pooled data across species and collapsed response categories down to those fish that herded in contrast to those that did not (pass under, hop, and rise combined), so as to render the data into a form most similar to our at-sea trawl-catch experiments. Again, ambient light (light or dark) mediated the influence of sweep height upon behavioral response ($G_{[1]}=5.75$, $P=0.017$). In Figure 5 we have simplified this relationship by graphing the percentage of fish herding under the two light and sweep height treatments. In addition to a conspicuous decrease in herding in the dark, elevation of the sweep decreased herding in the light but had little influence in the darkness—results consistent with those observed in the at-sea experiment.

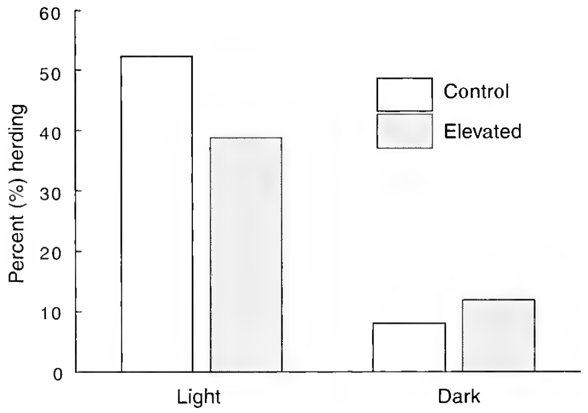

Figure 5

Percentage of fish that herded in response to simulated trawl sweep disturbance under both light and dark conditions, with the sweep both in contact (control) and elevated 10 cm off the bottom. Data were pooled across species and age classes.

Discussion

Ambient illumination controls many aspects of fish behavior, from feeding and habitat use (Janssen, 1978; Helfman and Schultz, 1984; Ryer and Olla, 1999; De Robertis et al., 2003; Petrie and Ryer, 2006) to social and antipredator behavior (Shaw, 1961; Ryer and Olla, 1998). Similarly, light has a pervasive influence upon interactions between fish and trawls. In this study, field data were largely consistent with our principal hypothesis; that trawls configured with sweeps that are in contact with the seafloor would catch more flatfish during the day than during the night. This pattern was observed for four out of six flatfish species examined: flathead sole, arrowtooth flounder, rock sole, and Alaska plaice. Herding, as seen in both roundfish and flatfish, is an ordered behavioral response in which fish move away from an approaching threat, i.e., the doors, sweeps, bridles, and wings of the net. Through either continuous swimming, or sudden swimming bursts, interspersed with rests on the bottom (Winger et al., 1999, 2004), fish then funnel to the center of the gear, where they concentrate before tiring and falling back into net. Several studies have demonstrated that both roundfish (Olla et al., 2000; Ryer and Olla, 2000) and flatfish (Ryer and Barnett, 2006) lose the ability to orient themselves in relation to gear and initiate herding when ambient light falls below the threshold for visual perception of the gear (Kim and Wardle, 1998a, 1998b).

Given the brief evolutionary time during which fish have interacted with towed fishing gear, approximately 100 years, it is unlikely that specific gear avoidance behavior has evolved. Rather, we consider it most parsimonious to assume gear avoidance is rooted in antipredator behavior. Although flatfish may initially erupt from the seafloor upon being disturbed by trawl ground-gear, as when attacked by a predator, subsequent herding behavior is consistent with "distance keeping" behavior, during which the fish attempts to maintain a safe distance between itself and a slowly pursuing predator. Scuba and skin divers who have attempted to follow fish along the seafloor are certainly familiar with this behavior. For flatfish, movement in the vertical dimension also plays a critical role during herding. It has been observed that flatfish remain close to the bottom during herding, usually less than half a body length (Ryer, 2008). Staying close to the bottom reduces drag, lessening thrust requirements to achieve a given speed—the ground effect (Videler, 1993; Gibson, 2005). Rising off the bottom makes flatfish more conspicuous, and due to the location of a flatfish's eyes, also interferes with visual tracking of a pursuing predator, in this case, the trawl ground-gear. Although they herd close to the bottom in the light, Pacific halibut and northern rock sole respond differently to ground-gear in the darkness, as demonstrated by laboratory experiments (Ryer and Barnett, 2006). Unable to see, the fish respond to contact with the ground-gear initially by hopping or swimming upward and away from the bottom. Similarly, in this study the percentage of fish moving off the bottom increased from 4% in the light to 21% in darkness, for all species and bar heights combined. Moving off the bottom in darkness probably functions as an antipredator tactic, making the flatfish more difficult to follow and may simply be the flatfish version of the Mauthner-cell triggered (lateral line) startle response (Eaton and Hackett, 1984).

Our second hypothesis, that elevation of sweeps off the bottom, 10 cm in this case, would decrease catch during daylight, but not at night, was also partially supported by our field experiment. Again, four of six flatfish species examined displayed the predicted catch pattern. Arguably, our analysis is based upon a small set of paired tows, particularly at night (n=5 pairs). Taken alone, these at-sea trials might not be convincing. However, these results were mirrored by our laboratory experiments, where the elevation of sweeps decreased herding to a greater extent in the light, compared to darkness. The elevation of sweeps had several consequences, all of which were likely to have influenced flatfish behavior. First, because most flatfish react to ground gear at a very short distance, often only after being struck, the likelihood that fish would simply not react and be passed over by sweeps was probably increased by sweep elevation. Further, part of the visual stimulus to herd that is associated with ground gear is the sand and mud cloud that is kicked up by the gear. This visual stimulus would be absent or greatly diminished by sweep elevation, further decreasing the likelihood of flatfish response. Our laboratory experiments with rock sole exhibited a pattern of response nearly identical to that seen in the field and indicated that passage under or over the gear was probably responsible for the decline in herding associated with sweep elevation during the day; in the light, fish passing beneath the sweep increased by 24% when the sweep was elevated. Lastly, even when herding is initiated, it must be maintained. Flatfish will sometimes dive under ground gear when they perceive a gap between the gear and the bottom—a trait that has been used to reduce flatfish bycatch (DeAlteris et al., 1997). Sweep elevation probably facilitated such escape. Unfortunately, our laboratory data were of little aid in evaluating this possibility. Because of the physical limitations of our apparatus, we characterized only the initial behavioral response of fish—not prolonged behavioral sequences that would characterize such deliberate escape tactics.

Our field data indicate that Pacific halibut could have a different pattern of availability or catchability, compared to that of the other flatfish species we examined. By virtue of size, Pacific halibut stand apart from most other flatfish. Beyond three or four years of age, their size likely renders them immune to most predators. This may make them more likely to venture from the bottom, as may their piscivorous diet. Consequently, they may be more likely than other species to rise off the bottom and swim back over sweeps. If so, it follows that most of the fish captured are those directly in the path of the net, excluding the area swept by the sweeps. Our trawling operations tended to produce larger, albeit not significant, Pacific halibut catches at night—a trend reported by commercial fishermen as well. It may be that with their greater speed and endurance, many halibut escape trawls during the day, but at night cannot see the gear to coordinate their escape. In contrast to the halibut results, the nonsignificant differences for yellowfin sole were similar in direction and magnitude to the significant differences detected for the other small flatfishes. This finding opens the possibility that these flatfishes had similar reactions, but our experiment just did not have the statistical power to detect them.

Diel patterns of catch in trawl fisheries and surveys reflect not only patterns in fish availability, but gear-specific behavioral influences upon catchability that are directly controlled by ambient illumination. Results of our laboratory experiments, along with earlier experiments (Ryer and Barnett, 2006), indicate that trawl footropes are likely to be more efficient at displacing flatfish from the bottom and rapidly transitioning them to the net under conditions of darkness (Ryer, 2008). In contrast, sweeps are probably more effective at herding flatfish inwards to the path of the net under daylight conditions. This disparity is probably responsible for the observed pattern of higher flatfish catches at night with survey nets, where bridles and sweeps are kept to minimal length, as compared to higher daytime catches with commercial flatfish nets and lengthy sweeps . These differences, as explained by the results of this work, highlight the importance of fish behavior for fish capture technology.

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Spatial and temporal variation in otolith chemistry for tautog (*Tautoga onitis*) in Narragansett Bay and Rhode Island coastal ponds

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Abstract—The elemental composition of otoliths may provide valuable information for establishing connectivity between fish nursery grounds and adult fish populations. Concentrations of Rb, Mg, Ca, Mn, Sr, Na, K, Sr, Pb, and Ba were determined by using solution-based inductively coupled plasma mass spectrometry in otoliths of young-of-the year tautog (*Tautoga onitis*) captured in nursery areas along the Rhode Island coast during two consecutive years. Stable oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) isotopic ratios in young-of-the year otoliths were also analyzed with isotope ratio mass spectrometry. Chemical signatures differed significantly among the distinct nurseries within Narragansett Bay and the coastal ponds across years. Significant differences were also observed within nurseries from year to year. Classification accuracy to each of the five tautog nursery areas ranged from 85% to 92% across years. Because accurate classification of juvenile tautog nursery sites was achieved, otolith chemistry can potentially be used as a natural habitat tag.

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The dependence of fish production and population dynamics on dispersal and migration among multiple habitats, referred to as "connectivity," is a critical property of marine populations. Connectivity rates determine colonization patterns for new habitats, the resiliency of populations to harvest, and can be used in the design of marine protected areas (MPAs). Quantifying connectivity rates in marine organisms is, however, extremely difficult because the natal and nursery origins of adults are almost unknown. Recently, tagging techniques with natural isotopic and elemental markers have been developed for species that were not able to be tagged or recaptured by conventional approaches. Chemical natural habitat tags in the otoliths of juvenile fish have been used to differentiate individuals from different estuarine and riverine systems (Thorrold et al., 1998a; Thorrold et al., 1998b; Gillanders and Kingsford, 2000; Gillanders, 2002b) and other types of nearshore habitats, such as estuary as opposed to rocky reef (Gillanders and Kingsford, 1996) and estuary as opposed to exposed coastal habitats (Yamashita et al., 2000; Forrester and Swearer, 2002). In addition, through chemical analysis of the juvenile core region of adult otoliths, natural habitat tags have been used to determine the proportion of the adult population that resided in different juvenile habitats (Yamashita et al., 2000; Thorrold et al., 2001; Gillanders, 2002a).

The tautog (*Tautoga onitis*) is an economically and ecologically important species found in the waters of eastern North America from the Gulf of Maine to North Carolina. Juvenile tautog are known to depend on shallow water habitats where they are safe from high levels of predation and can find necessary food resources (Dorf and Powell, 1997; Arendt, 1999). However, the relative importance of open coastline and enclosed bays and lagoons as nursery habitat for tautog is still poorly understood (Sogard et al., 1992). In light of the fact that the northeastern coast of the United States has experienced a major loss of its estuarine habitats because of human alteration of the coastal zone (Bromberg and Bertness, 2005), data are needed to quantify the importance of specific coastal habitat types in sustaining tautog populations.

Our long-term goal is to investigate the utility of naturally occurring habitat tags to determine habitat linkages in Narragansett Bay and other nearby estuarine systems by juvenile tautog. This is an initial crucial step to quantify the relative contribution of estuarine habitats for the population connectivity of adult tautog.

Materials and methods

Sampling of juvenile fish

In Rhode Island, young-of-the-year (YOY) tautog of 45–64 mm fork length (FL) were sampled from three sites in Narragansett Bay: Mt. Hope Bay (MH), Gaspee Point (GP), and Rose Island (RS); and from two sites from the coastal ponds along the Rhode Island southern shore: Point Judith, lower pond (PJ), and Charlestown Pond (CP) (Fig. 1). The samples were obtained in cooperation with Rhode Island Department of Environmental Management, Division of Marine Fisheries (RIDEM), during August and September of 2005 and 2006. The sampling stations were selected to include different nursery areas and possibly different chemical backgrounds and according to information on juvenile tautog abundance from RIDEM. Average monthly surface temperatures and salinities at Gaspee Point for 2005 were 22°C and 24.9‰, and for 2006 were 20.6°C and 22.5‰. For Mount Hope Bay, average surface temperatures and salinities were 21.7°C and 27.0‰, and for 2006 were 20.5°C and 24.9‰. Data from the closest point to Rose Island showed average surface temperatures and salinities for 2006 were 17.4°C and 30.8‰. Twenty juveniles per site per year were captured for analysis. Sampled fish were kept frozen until dissection for the removal of otoliths.

Laboratory processing of samples

Before dissection, each fish was weighed (wet weight to the nearest 0.1 g) and measured (FL and standard length [SL] to the nearest 0.1 mm). Both sagittal otoliths were removed from each fish, cleaned of adhering tissue, rinsed 3× with Milli-Q–filtered (Millipore Corp., Billerica, MA) water, and allowed to dry in a class-100 laminar-flow hood. The left sagittal otolith was used for trace metal analysis and the right otolith was used for stable isotope analysis. A total of 164 otoliths were prepared for trace metal analysis. Each otolith was weighed on a Thermo Cahn microbalance (± 0.01 mg) (Thermo Fisher Scientific, Waltham, MA). Samples were then placed in acid-washed 2.5-mL snap-cap polypropylene containers. The otolith weights ranged from 0.08 to 0.34 mg and averaged 0.18 mg. Otoliths for trace metal analysis were transferred to 5-mL clean polypropylene tubes and 0.2 mL of triple-distilled 17% HNO_3 was added to insure complete dissolution (in about 30 seconds). An internal thulium single-element standard spike was added (to correct for variable matrix effects during the inductively coupled plasma mass spectrometry analyses) and then the solution was diluted to 1.8 mL with triple-distilled water. This dilution resulted in a Ca concentration of approximately 40 ppm in the analyzed otolith solution.

Otolith chemistry

Elemental concentrations of YOY otoliths were determined through solution-based ICPMS at the University of Rhode Island Graduate School of Oceanography. All measurements were carried out on a Finnigan element high-resolution inductively coupled plasma mass spectrometer (HR-ICPMS) (Thermo Fisher Scientific, Waltham, MA). A procedural blank was prepared in the same manner as had been used for the other samples, but with no otolith present. The procedural blank was compared to the system blank to determine if contamination occurred during processing. System blanks were made from the same acid used for sample dissolution and were run every four samples. A drift-correction standard was prepared by gravimetrically spiking a $CaCO_3$ standard solution with the appropriate concentrations of Na, K, Rb, Mg, Ca, Mn, Ni, Cu, Zn, Sr, Ba, Co, and Pb to match the typical elemental composition of the otoliths. This drift-correction standard was analyzed every four samples to track and correct for variations in instrument sensitivity during each analytical time period. The choice of these thirteen elements for our study was based on previous studies of elemental composition of juvenile fish otoliths. Analytical results were expressed as absolute concentrations of elemental molar ratios with respect to calcium: Element:Ca ratios, expressed as units of mmol/mol or µmol/mol.

The elements that were always above detection limits (Rb, Mg, Ca, Sr, and Ba) were used for subsequent analysis. The average relative standard deviations were as follows: Rb (3%), Mg (10%), Ca (1%), Sr (1%), and Ba (5%). The limits of detection were as follows (values in ppm): Rb (0.007), Mg (0.02), Sr (0.077), and Ba (0.014). The detection limits for the whole otolith dissolution-solution–based method were calculated as three times the standard deviation of the counts per second (cps) of the isotope of interest in acid blanks divided by the sensitivity in cps/ppm of the CRM22 carbonate standard. For every isotope, these were in the sub-ppm range— a result that compares with the 3 to 2000 ppm range of the elements of interest in the sample otoliths.

Stable carbon and oxygen isotopes of these otolith samples were determined at Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, by using an automated carbonate device (Kiel III) attached to a thermo Finnigan delta-plus stable isotope mass spectrometer (Thermo Fisher Scientific, Waltham, MA). Data were expressed by using conventional δ notation

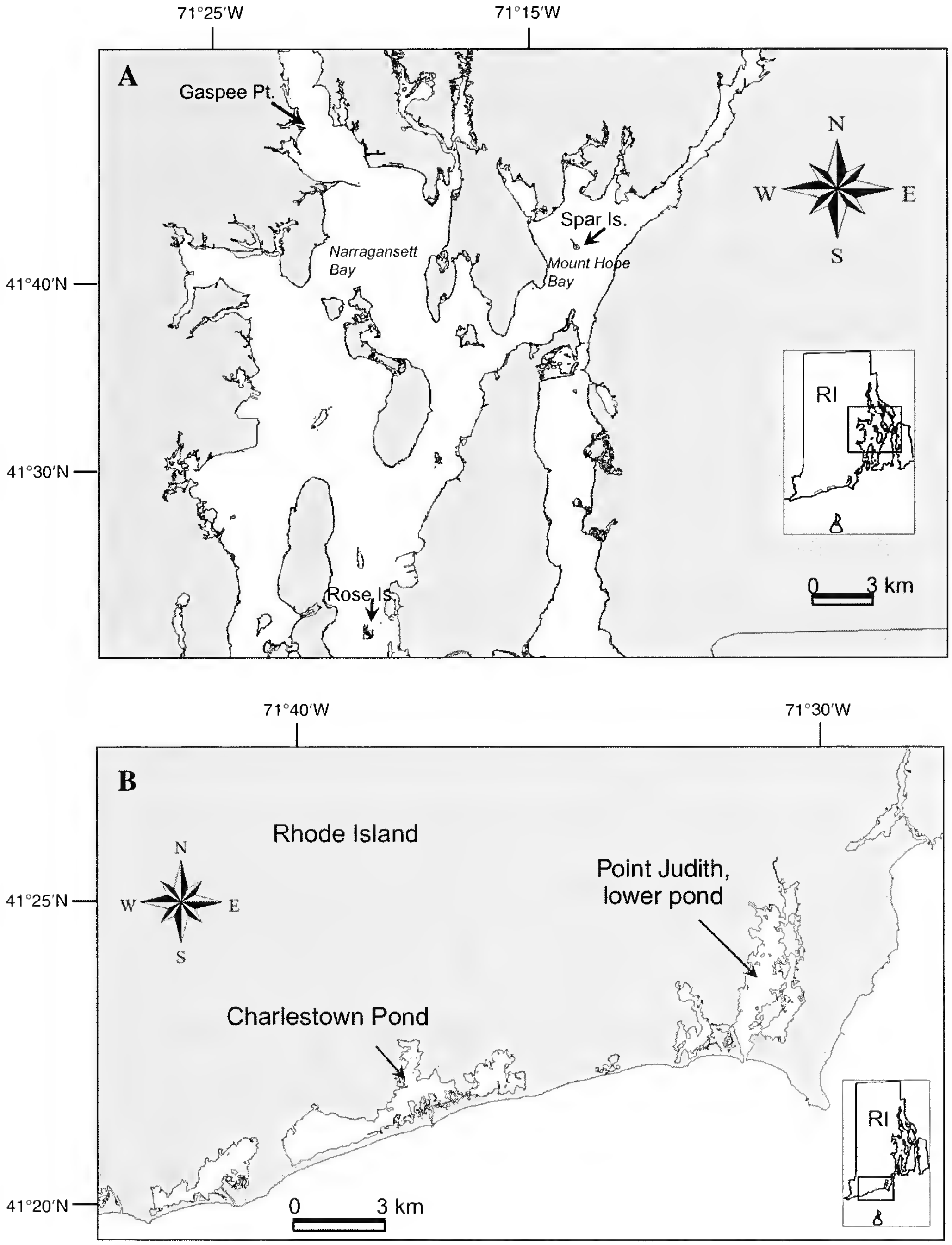

Figure 1

(**A**) Map of tautog (*Tautoga onitis*) sampling stations in Narragansett Bay for 2005 and 2006 that were surveyed for juvenile otolith element concentrations and isotopic signatures. Sampling stations are shown in arrows. (**B**) Map of the south coast of Rhode Island showing two coastal ponds (Charlestown, Point Judith) that were surveyed for tautog for years 2005 and 2006 to determine otolith element concentrations and isotopic signatures. Sampling stations are shown in arrows.

in relation to V-PDB (Vienna Peedee Belemnite). Data were corrected for the usual isobaric interferences. The external precision (calculated from replicate analyses of an internal laboratory calcite standard) was 0.04% for $\delta^{13}C$ and 0.08% for $\delta^{18}O$.

Statistical analysis

Two-way analysis of variance (ANOVA) was used to test for differences in fish body length among stations and years. We also examined relationships between otolith

Table 1

Average size distribution of tautog (*Tautoga onitis*) collected in Rhode Island for analysis of otolith elemental concentrations and stable isotopic signatures. The numbers of fish measured at each station (*n*) to obtain average fork lengths (FL in mm) in each year are shown. Numbers in parentheses are standard errors.

	2005		2006	
Station	*n*	FL	*n*	FL
Gaspee Point (GP)	17	59.6 (1.2)		
Mount Hope Bay (MH)	17	59.1 (2.1)	21	63.0 (2.9)
Rose Island (RS)	20	52.1 (1.2)	17	45.3 (3.5)
Point Judith, lower pond (PJ)	18	49.4 (2.1)	19	57.3 (1.5)
Charlestown Pond (CP)	17	50.2 (3.0)	18	54.9 (2.7)

weight and otolith elemental composition and isotopic signatures with analysis of covariance (ANCOVA). If there was a significant relationship, we removed the effect of size (otolith weight used as a proxy for fish size) to ensure that differences in fish size among samples did not confound any site-specific differences in otolith chemistry. Concentrations of elements were weight-detrended by subtraction of the product of the common within-group linear slope multiplied by the otolith weight from the observed concentration (Campana et al., 2000).

To detect differences in the concentrations of particular elements and multi-element fingerprints among stations and between years, we performed ANOVA and multivariate analyses of variance (MANOVA). Pillai's trace statistic was chosen as the multivariate test statistic because it is more robust than other multivariate statistics (Wilkes's lamda, Hotelling's T-test) to small sample sizes, unequal cell sizes, and situations in which covariances are not homogeneous. Tukey's HSD test was used to detect *a posteriori* differences among means ($\alpha=0.05$). Before statistical testing, residuals were examined for normality and homogeneity among stations. To meet model assumptions, all analyses were performed on natural log-transformed data. We also used linear discriminant function analyses (DFAs) on tautog juvenile data to visualize spatial differences in juvenile otolith chemistry data within sites and to examine classification success for juveniles from different sites or regions. Classification success is the percentage of fish that are correctly assigned to their actual region given the information on location where the fish was collected and the chemical signature of each fish. Cross validations were performed by using jackknife ("leave one out") procedures in SYSTAT (vers. 11, Systat Software, Inc., Chicago, IL).

Results

Size distribution

Mean (FL) of juvenile tautog at stations in Rhode Island ranged from 45 to 63 mm (Table 1). There were significant differences in mean length among stations (ANOVA, $P<0.001$) and between years (ANOVA, $P<0.05$) within Rhode Island stations. There were no significant differences in mean FL among stations within Narragansett Bay. However, in 2005, mean FL from all stations within Narragansett Bay were significantly longer than that for individuals caught in the coastal ponds (Point Judith, lower pond, Charlestown Pond) (Tukey test, $P<0.05$). In 2006; only Mount Hope Bay had fish significantly longer than those from Rose Island (Tukey test, $P<0.05$).

Otolith chemistry

Results of MANOVA showed that the chemical signatures of trace metals and stable isotopes combined in tautog otoliths differed significantly among stations (MANOVA, $F_{18,384}=20.72$, $P<0.001$) and years (MANOVA, $F_{6,126}=9.05$, $P<0.001$) within Rhode Island. Significant interaction between station and year (MANOVA, $F_{18,384}=5.18$, $P<0.001$) implied that chemical signatures differed between years depending on the station studied. Classification success for tautog by using both trace metals and stable isotopes for stations within Rhode Island for each of the two years ranged from 85% to 92% (Table 2).

Individual elemental concentrations

In Rhode Island, one trace element (Rb) and one stable isotope ($\delta^{13}C$) showed significant relationships with the covariable otolith weight in the ANCOVA ($P<0.001$) and therefore required the effect of otolith weight be removed for subsequent ANOVA analysis. The elemental concentrations and isotope signatures varied significantly among stations (ANOVA, $P<0.001$), and between years (ANOVA, $P<0.001$) (Fig. 2). Significant interaction between station and year (ANOVA, $P<0.001$) indicated that concentration of individual elements differed between years depending on the station studied. In Rhode Island, elemental concentrations of Sr, Ba, Mg, Rb, and the stable isotopes $\delta^{13}C$ and $\delta^{18}O$ varied significantly among stations in 2005, whereas only Ba

Table 2

Classification success (as a percentage) results determined by jack-knife cross validation procedure for linear discriminant function analysis of chemical concentrations in tautog (*Tautoga onitis*) otoliths collected at Rhode Island stations in 2005 and 2006, with the use of solution-based inductively coupled plasma mass spectrometry for the combined trace metals (Sr, Ba, Mg, Rb): [Sr/Ca], [Ba/Ca], [Rb/Ca], [Mg/Ca]) and for $\delta^{13}C$ and $\delta^{18}O$ stable isotopes. Names of the stations are Gaspee Point (GP), Mount Hope Bay (MH), Rose Island (RS), Point Judith, lower pond (PJ), Charlestown Pond (CP).

	GP	MH	RS	PJ	CP	Classification success (%)
2005						
GP	14	0	0	0	1	93
MH	0	13	0	2	1	81
RS	0	0	19	1	0	95
PJ	0	0	0	16	1	94
CP	0	1	0	0	16	94
Total	14	14	19	19	19	92
2006						
GP	0	0	0	0	0	
MH	0	13	0	2	1	81
RS	0	0	14	2	1	82
PJ	0	2	0	15	0	88
CP	0	0	0	2	15	88
Total		15	14	21	17	85

and $\delta^{18}O$ varied significantly among stations in 2006 (ANOVA, $P<0.001$) (Fig. 2). For example, $\delta^{18}O$ was highest at Rose Island at the mouth of Narragansett Bay, whereas $\delta^{13}C$ magnitudes were similar across years for all Narragansett Bay stations. Sr concentrations within Narragansett Bay and the coastal ponds also remained similar in magnitude throughout the years of study.

Discussion

The elemental composition of juvenile tautog otoliths varied considerably within and among estuaries and between years. We found very strong differences in the concentrations of Mg, Sr, Ba, and Rb, as well as in the stable isotopic signatures of $\delta^{13}C$ and $\delta^{18}O$, among stations within RI. High classification success rates (generally >85%) of the discriminant functions derived from trace element and stable isotope signatures together confirmed their use as an effective natural tag of the estuarine nursery area of juvenile tautog. Although most of the variance in trace element signatures was concentrated among estuaries, we also found significant differences in elemental fingerprints and stable isotopes in tautog otoliths among sites about 10 to 25 km^2 apart within Narragansett Bay resulting in 100% classification success within that water body. These data indicate that the physicochemical characteristics of specific sections of the estuaries may vary enough to generate the differences in otolith chemistry that we observed within each estuary.

Elemental fingerprints, however, should not be regarded as permanent markers of actual estuarine habitat or environment (Forrester and Swearer, 2002; Swearer et al., 2003). Estuarine habitats are very dynamic; seawater properties and composition at a particular location can vary over tidal to annual time scales (Peters, 1999). As a result, it may be expected that the magnitude of variations in elemental fingerprints in otoliths among estuaries will not remain constant over time. The significant interannual differences we report among year classes in age-0 tautog otolith elemental signatures is similar to interannual differences in otolith chemistry reported for other marine fishes (Gillanders and Kingsford, 2000; Gillanders, 2005). Thus, interannual differences indicate that age-0 tautog elemental signatures must be analyzed on a year-class–specific basis because there were stations where concentrations were not consistent between years.

It is not surprising to see such clear differences in otolith chemical signatures among the stations sampled in Narragansett Bay. Data from RIDEM show that there were also significant differences in salinity regimes in these regions during the late spring and summer of 2005 and 2006 (H. Stoffel, and J. McNamee, unpubl. data[1]). The proximity of Rose Island station to the mouth of Narragansett Bay meant that high salinities (up to 30‰) would be observed. On the other hand, the lower-salinity stations within the upper region of Narragansett Bay are located much closer to the industrial area and watershed and therefore potentially more prone to terrestrial influences from freshwater runoff resulting in reduced salinities (20–25‰).

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[1] Stoffel, H., and J. McNamee. 2008. Rhode Island Dept. Environmental Management (RIDEM), Jamestown, RI 02879.

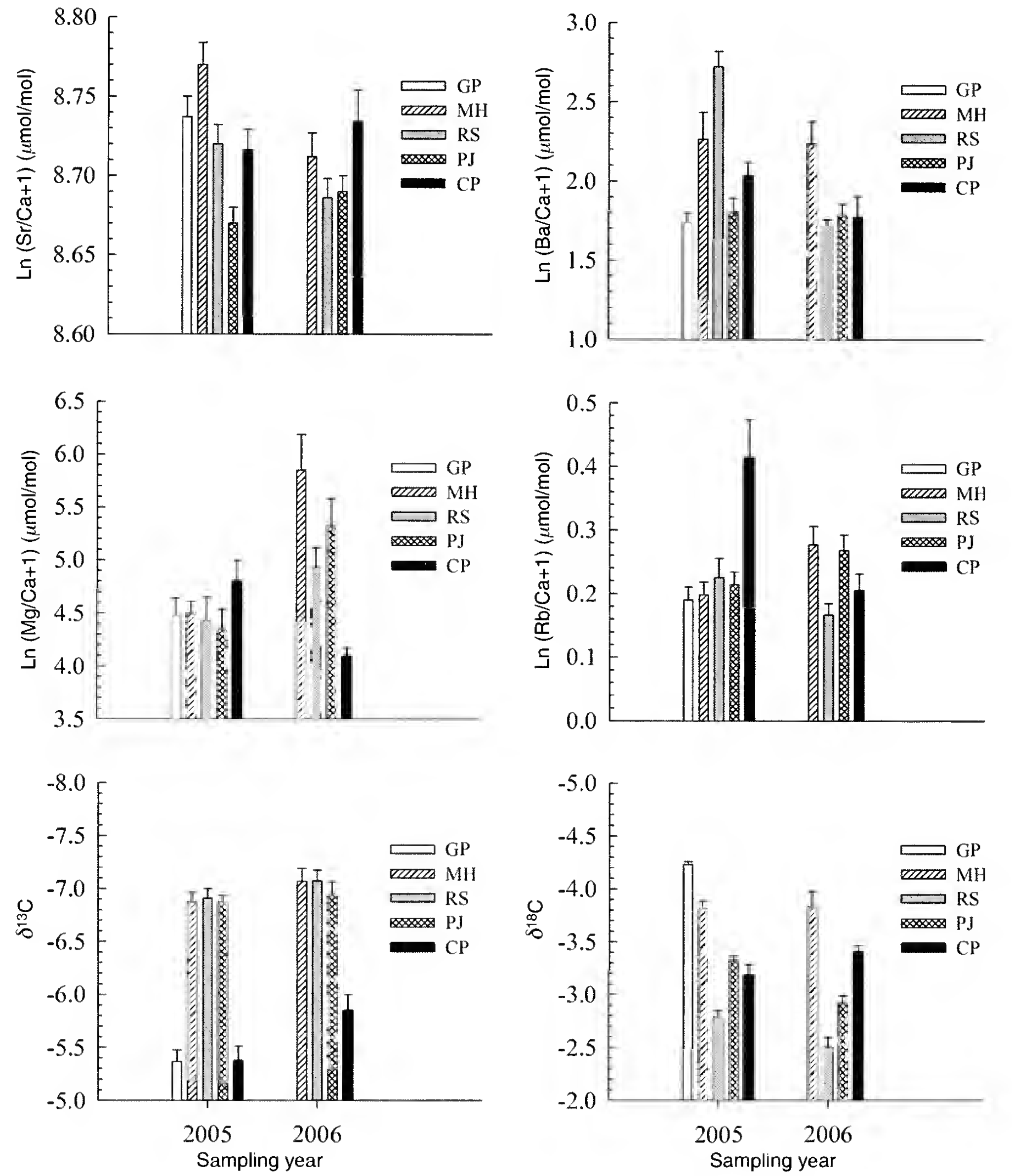

Figure 2

Variation in trace elements and stable isotopes concentrations measured in otoliths of young-of-the-year tautog (*Tautoga onitis*) collected in Rhode Island in 2005 and 2006. All trace element data (element/Ca×10^6) are ln(x+1) transformed. Rhode Island station codes are GP=Gaspee Point, MH=Mount Hope Bay, RS=Rose Island, PJ=Point Judith, lower pond, and CP=Charlestown Pond.

Successful discrimination between estuarine nurseries in the present study was accomplished through otolith elemental fingerprints, fulfilling one of the requirements for their possible use as natural tags (Campana et al., 2000). The estuarine nursery origin of juvenile tautog was accurately identified based on otolith elemental fingerprints and stable isotopes. Several methods based on laser ablation (Thorrold et al., 2001; Gillanders, 2002a) or micromilling techniques (Gillanders and Kingsford, 1996; Gillanders, 2005; Brown, 2006) could be used to determine elemental fingerprints found in the otolith cores of adult tautog for comparison with the juvenile estuarine fingerprints that we have established. We believe solution-based techniques are more suitable than microprobe techniques for analysis of tautog otolith elemental concentrations because 1) solution-based techniques tend to have higher sensitivity, accuracy, and precision compared to microprobe techniques (Campana, 1999; Campana et al., 2000); and 2) solution-based techniques can provide more precise natural tags on fish with limited movement within habitats during their first year of life. For example, tautog have a short larval period of 15 to 20 days (Sogard et al., 1992; Dorf and Powell 1997) and once larvae have settled, they have small home range of approximately 20 meters (Able et al., 2005) during their first year of life. Thus, juvenile cores samples from age classes representing fish born in 2005 and 2006 could be extracted by micromilling procedures and their chemical elements can be analyzed by solution ICPMS. Present results are a step towards establishing juvenile movement to adult habitats, which must be examined in nursery studies (Beck et al., 2001). Identifying links between juvenile and adult habitats, and understanding connectivity between estuarine nurseries and adult populations, has the potential to aid fishery managers and aid in the management and conservation of estuarine fish nursery habitats.

Acknowledgments

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Abstract—We evaluated the effectiveness of wooden artificial reefs (ARs) as fish habitat. Three types of ARs, made of cedar logs, broadleaf tree logs, and PVC pipes, respectively, were deployed in triplicate at 8-m depth off Maizuru, Kyoto Prefecture, Sea of Japan, in May 2004. Fish assemblages associated with each of the nine ARs were observed by using SCUBA twice a month for four years. Fish assemblages in the adjacent habitat were also monitored for two years before and four years after reef deployment. In the surveyed areas (ca. 10 m^2) associated with each of the cedar, broadleaf, and PVC ARs, the average number of fish species was 4.14, 3.49, and 3.00, and the average number of individuals was 40.7, 27.9, and 20.3, respectively. The estimated biomass was also more greater when associated with the cedar ARs than with other ARs. Visual censuses of the habitat adjacent to the ARs revealed that the number of fish species and the density of individuals were not affected by the deployment of the ARs. Our results support the superiority of cedar as an AR material and indicate that deployment of wooden ARs causes no reduction of fish abundance in adjacent natural reefs.

Fish assemblages associated with three types of artificial reefs: density of assemblages and possible impacts on adjacent fish abundance

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Habitat complexity plays a major role in the survival of young demersal fishes by providing a refuge from predation (Ferreira et al., 2001; Scharf et al., 2006; Hamilton and Konar, 2007). Fish species richness is highly dependent on the rugosity and variety of growth forms in the habitat, whereas the height of vertical structures is an important predictor of total fish abundance (Gratwicke and Speight, 2005). In this respect, artificial reefs (ARs) are often deployed to improve the quality of habitat (Gorham and Alevizon, 1989). In addition to their role as refuges, ARs host encrusting invertebrates that can be consumed as prey by fishes (Seaman and Jensen, 2000). Fish are often more abundant at ARs than at natural reefs, probably because the vertical structures potentially allow more varied refuges for fish settlement and recruitment than the usual more moderately sloped bottoms of natural reefs (Rilov and Benayahu, 2000; Reed et al., 2006).

Although the deployment of structures functioning as ARs may well have started long ago by fishermen in various localities around the globe, research on this subject is relatively recent (Seaman and Sprague, 1991). Two countries, United States and Japan, have relatively long histories of nationwide projects on ARs. In the case of the United States, the main goal of deploying ARs has been to improve catch for recreational fishermen. Common materials used for these ARs have been waste products, such as automobiles, tires, and oil and gas platforms. The use of such products has caused environmental concerns, resulting in a shift toward the construction of ARs with concrete (Collins et al., 2002). In contrast, the purpose of Japanese deployments of ARs have primarily been to improve commercial fishery production, and governmental agencies have invested heavily in the construction of large ARs made of concrete and steel to be deployed in coastal areas.

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The recent trend for ARs in Japan has shifted from concrete to wooden construction. This has been partly due to funding shortages, but also because fishermen have found that wooden ARs attract fish more rapidly than those made of concrete or steel. Indeed, most coastal prefectures in Japan deploy wooden ARs with or without governmental subsidies under the supervision of local fishermen's cooperatives. The materials and shape of wooden ARs differ depending on each fishery cooperative. As much as 70% of the land area in Japan is forested, half of which is plantation forests of conifers, such as Japanese cedar (*Cryptomeria japonica*) and hinoki cypress (*Chamaecyparis obtusa*). Although these forests require occasional thinning, many of them lack such maintenance because of the decline in the market price of timber. Therefore, the construction of wooden ARs also has the socioeconomic potential to stimulate the demand for forestry materials.

The primary goal of the present study was to confirm the efficacy of wooden ARs, especially those made of cedar tree logs as fish habitat. For this purpose, fish assemblages associated with ARs made from cedar trees were compared to those made from broadleaf trees and those made with polyvinyl chloride (PVC) pipes. There is a debate whether ARs merely attract fishes from adjacent areas or whether they do improve fishery productivity (Grossman et al., 1997; Pickering and Whitmarsh, 1997). We therefore tested the possibility that ARs attract fishes from adjacent areas and thus concentrate fish abundance at the ARs, rather than fish abundance is spread over the fishing ground as a whole. A visual census had been conducted twice a month for more than two years before the deployment of these ARs in adjacent areas; hence the fish fauna was compared in the area before and after the deployment of ARs.

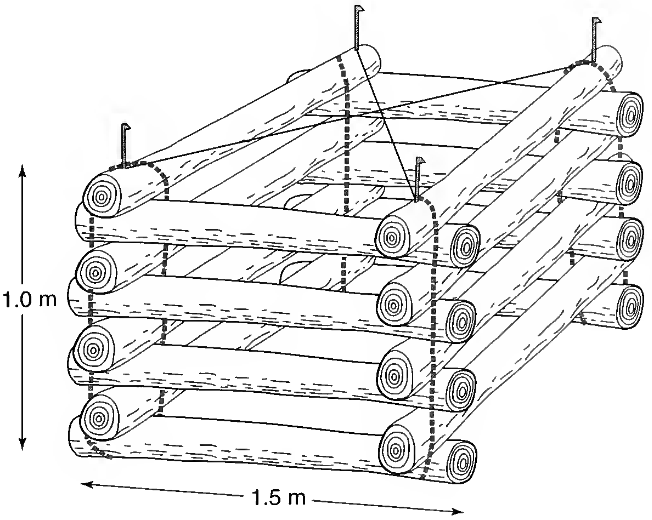

Figure 1

Shape and dimensions of the artificial reefs installed off Maizuru, Kyoto, in 2004 to evaluate the effectiveness of cedar, broadleaf, and PVC artificial reefs.

Materials and methods

Deployment and visual census of artificial reefs

Three types of ARs were prepared. The design of the ARs was modified from that designed by the Atake Forestry Association, Yamaguchi, Japan (http://www.geocities.jp/abu_kikori/katsudou/gyosyou/gyosyou2.html, accessed on December 2003; also see Fig. 1). The first type of AR (cedar AR) was constructed of 16 log sections (1.5 m long, 6.9–18.4 cm diameter) of Japanese cedar (*Cryptomeria japonica*) arranged in a parallel cross formation. Each corner was tied with rope and fixed with a stainless steel rod. Diagonal wires helped maintain the rectangular shape. The second type of AR (broadleaf AR) was constructed from six species of broadleaf trees harvested from the Ashiu Forest Research Station, Kyoto University, and assembled with the same dimensions as those used for the cedar AR. The broadleaf tree species used were Japanese cherry birch (*Betula grossa*), hornbeam (*Carpinus laxiflora*), Japanese beech (*Fagus crenata*), Chinese chestnut (*Castanea crenata*), redvein maple (*Acer rufinerve*), and macropoda holly (*Ilex macropoda*). The diameter of broadleaf and cedar logs ranged from 7.5 to 19.2 cm. The third type of AR (PVC AR) was made of hollow PVC pipes (11.8 cm diameter, 3 mm thickness) and was assembled in the same manner as that used for the other two types of ARs.

These three types of ARs were constructed in triplicate and deployed at a depth of 8 m off the Maizuru Fisheries Research Station (MFRS), Nagahama, Maizuru, Kyoto (35°29′N lat. and 135°22′E long.) on 21 May 2004 (Fig. 2). The shore in this area is a concrete bank and its subtidal zone consists of natural rocks, concrete blocks, both partly covered by live oyster (*Crassostrea gigas*) and their dead shells, and sandy silt with some macroalgal vegetation. The substrate in the research area consisted of muddy silt with no macroalgae vegetation. Each AR was sunk with 240 kg of sand bags (60 kg attached to each corner of the AR). ARs were set 15 m apart.

Twice monthly visual censuses of fish assemblages associated with each AR were conducted for four consecutive years after AR deployment. All census observations were made by the first author with SCUBA equipment. The area in and around each AR was observed for about three minutes and the species, size, and number of fish were recorded. A census commenced from one of the lateral sides of an AR and extended out to about 1 m from each side. The observer then swam around and above the AR, and the fish inside the AR were

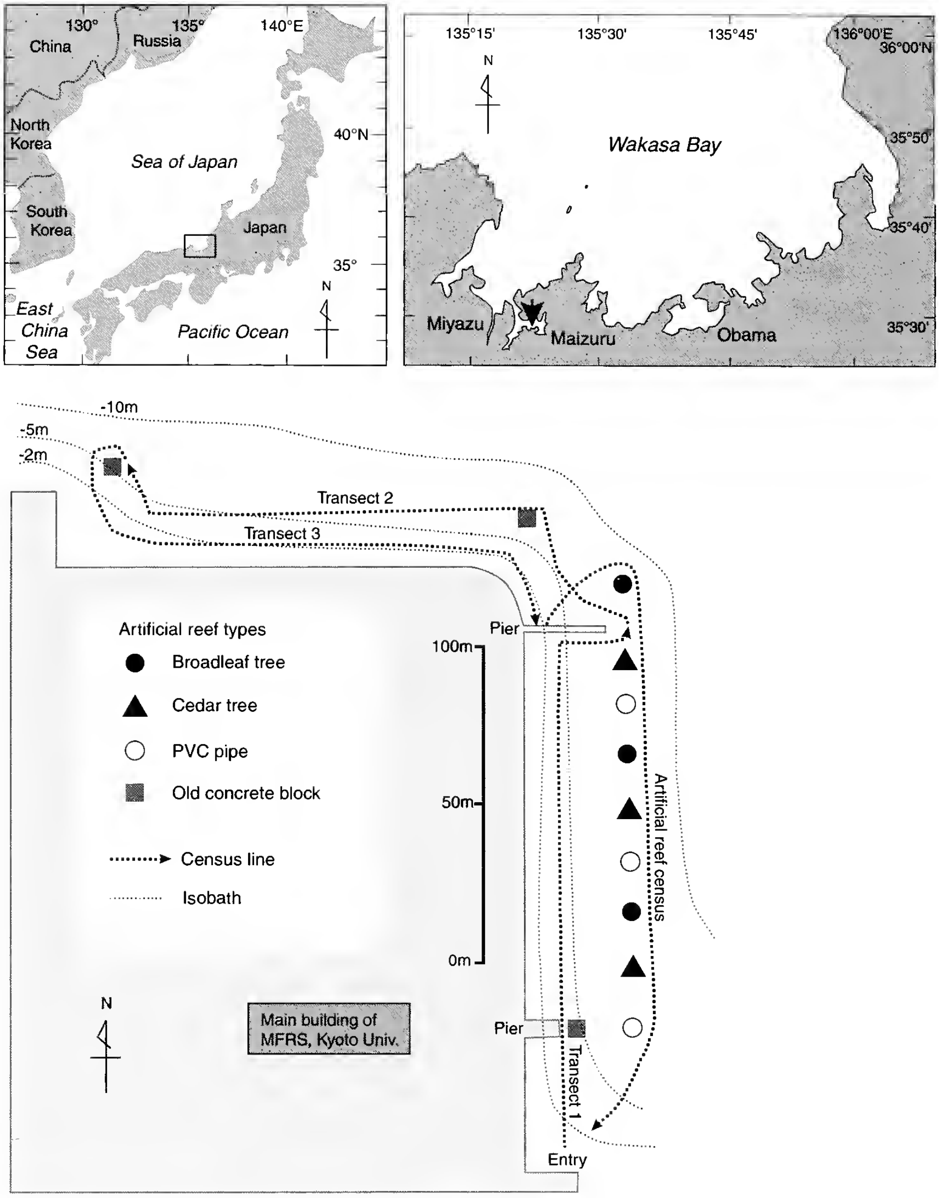

Figure 2

Map of study area for artificial reef deployment off Maizuru, Kyoto, in 2004. Upper-left map shows location of Wakasa Bay (in box) along the Sea of Japan. The arrow in the upper-right map represents the location of the research area in Maizuru Bay. Lower map shows the research area off the Maizuru Fisheries Research Station (MFRS), Kyoto University, with the nine artificial reefs (three types×three replicates) deployed in a line. Observations were conducted after the visual census of the adjacent habitat (transects 1–3). Census lines are expressed by thick dotted lines, and -2 m, -5 m, and -10 m isobaths are expressed by thin dotted lines.

recorded. Fish were considered as associating with an AR if they were swimming or dwelling within 1 m of the AR (Sherman et al., 2002), and thus fish in an area of about 10 m^2 were counted for each AR. Fish standard length (SL) was estimated with the help of a scale marked on a clipboard and was recorded. Length estimates were occasionally calibrated by capturing and measuring fish. These calibrations revealed that visual SL estimates were within 10% error of the actual measured SL. Water temperature and visibility during observations ranged from 10.1° to 28.8°C and from 1 to 5 m, respectively. Biomass calculation for each AR was conducted according to the method of Santos et al. (2005) and Friedlander et al. (2007). The estimated average length of each species for each sample was converted to mass by using the length-mass relationship

$$M=a\mathrm{SL}^b,$$

where a and b = constants for allometric growth;
SL = standard length; and
M = mass.

Length-mass parameters were obtained from FishBase (www.fishbase.org, accessed on July 2008) and calibration was based on our own samples.

The number of fish species (species richness), total number of fish individuals (abundance), total fish biomass, and number of individuals of each fish species associated with each type of AR were compared among the three types of ARs by repeated measures ANOVA followed by Tukey's HSD test. Data for the number of fish individuals and their biomass were log (x+1) transformed to obtain homoscedasticity.

Estimation of the impact of AR deployment on fish abundance in the adjacent area

Fish assemblages in the area surrounding the ARs were compared before and after AR deployment. Data from the twice monthly visual censuses in each area were used for this purpose (Masuda, 2008; Fig. 2). The number and size of fish of each species found along three 400-m^2 belt transects have been recorded twice a month since 1 January 2002. One transect was close to the location of the ARs that we deployed in the present study (transect 1), and the other two were relatively distant (transects 2 and 3). Therefore, species richness and fish abundance in transect 1 would decline after AR deployment if fish were simply attracted from the adjacent natural reef to these ARs. Each of the three transects included areas of rocky reef, live oysters and their dead shells, a sandy or muddy silt bottom, and an artificial vertical structure made of concrete blocks that had been deployed more than 20 years earlier. The size (length × width × height) of the concrete structures along transects 1, 2, and 3 were 0.5×3×2.4 m, 1.8×3×1 m, and 2.5×2.5×2 m, respectively. Data from 23 May 2002 to 15 May 2004, and those from 29 May 2004 to 8 May 2008 were used to compare the fish assemblages before and after deployment of the ARs. Analyses of covariance (ANCOVA) was used to compare species richness and fish abundance in each transect before and after deploying the wooden or PVC ARs, and bottom water temperature was used as a covariant because fish species richness and abundance increase almost linearly with the increase of bottom water temperature in this habitat (Masuda, 2008). The number of individuals of each species was also compared by ANCOVA before and after deployment of the ARs. All statistical analyses were conducted with the software JMP (vers. 5.0.1J, SAS Institute, Inc., Cary, NC) with an alpha level of 0.01.

Table 1

The mean (±standard error) number of species, individuals, and estimated biomass of fish attracted to the cedar, broadleaf, and PVC artificial reefs over the entire observation period (2004–08) and for each of the four years (n=3 ARs per type). Different letters represent significant differences among AR types (P<0.01, Tukey's HSD test).

	Cedar ARs	Broadleaf ARs	PVC ARs
No. of species			
Whole period	4.14 ± 0.138^a	3.49 ± 0.107^b	3.00 ± 0.113^c
1st year	5.14 ± 0.332^a	3.44 ± 0.245^b	2.51 ± 0.201^c
2nd year	4.10 ± 0.289^a	3.49 ± 0.244^b	2.83 ± 0.232^c
3rd year	3.93 ± 0.226^a	3.63 ± 0.225^{ab}	3.28 ± 0.217^b
4th year	3.38 ±0.196	3.40 ±0.193	3.38 ±0.195
No. of individuals			
Whole period	40.7 ± 4.43^a	27.9 ± 2.88^b	20.3 ± 2.18^c
1st year	84.5 ± 12.9^a	36.8 ± 5.86^b	29.6 ± 6.23^c
2nd year	24.1 ± 5.00^a	28.0 ± 5.88^a	10.9 ± 2.25^b
3rd year	32.1 ± 8.31^a	24.7 ± 6.80^b	19.0 ± 4.00^b
4th year	22.0 ±4.59	22.1 ±4.15	21.9 ±3.82
Fish biomass (grams)			
Whole period	284 ± 34.7^a	143 ± 19.1^b	157 ± 40.7^b
1st year	498 ± 89.8^a	113 ± 24.4^b	243 ± 157^b
2nd year	222 ±51.6	134 ±38.7	89.1±19.3
3rd year	310 ±82.0	179 ±44.8	141 ±28.4
4th year	108 ± 29.9^b	148 ± 41.8^b	155 ± 28.2^a

Results

Fish assemblages associated with the ARs

Both species richness and fish abundance were highest associated with the cedar ARs, intermediate with the broadleaf ARs, and lowest with the PVC ARs when compared over the entire sampling period (Table 1). These differences were significant among the three AR types in both of these measurements (repeated measures ANOVA followed by Tukey's HSD test: P<0.01). The greater effectiveness of the cedar ARs was prominent in the first year after deployment but decreased with time and became nonsignificant in the fourth year (Table 1; Fig. 3). Fish biomass was greatest in the cedar and PVC ARs in the first and fourth year, respectively, but did not differ significantly in the second and third years.

A total of 62 fish species were observed in 96 dives on these nine ARs, among which six species were found most frequently in the cedar ARs, two in the broadleaf ARs, and two in the PVC ARs (Table 2). Five most commonly observed fish species in the ARs were black rockfish (*Sebastes inermis*), jack mackerel (*Trachurus japonicus*), bambooleaf wrasse (*Pseudolabrus sieboldi*), chameleon goby (*Tridentiger trigonocephalus*) and whitespotted pigmy filefish (*Rudarius ercodes*) (Fig. 4); the former three species are targeted in commercial fisheries, whereas the latter two are prey species of other commercial species. Jack mackerel is pelagic and migratory, and the other four species are demersal and relatively sedentary. The typical fishes showing high preference for the cedar ARs were black rockfish, sunrise sculpin (*Pseudoblennius cottoides*), black sea bream (*Acanthopagrus schlegelii*), whitespotted pigmy filefish, thread-sail filefish (*Stephanolepis cirrhifer*), and finepatterned puffer (*Takifugu poecilonotus*). Two species of goby (*Istigobius hoshinonis* and *T. trigonocephalus*) were most abundant in the broadleaf ARs (Fig. 4). Redspotted grouper (*Epinephelus akaara*) and barface cardinalfish (*Apogon semilineatus*) were most abundant in the PVC ARs. Jack mackerel and bambooleaf wrasse were the most abundant species during the entire census period (Table 2), but they did not show any clear preference for a particular type of AR.

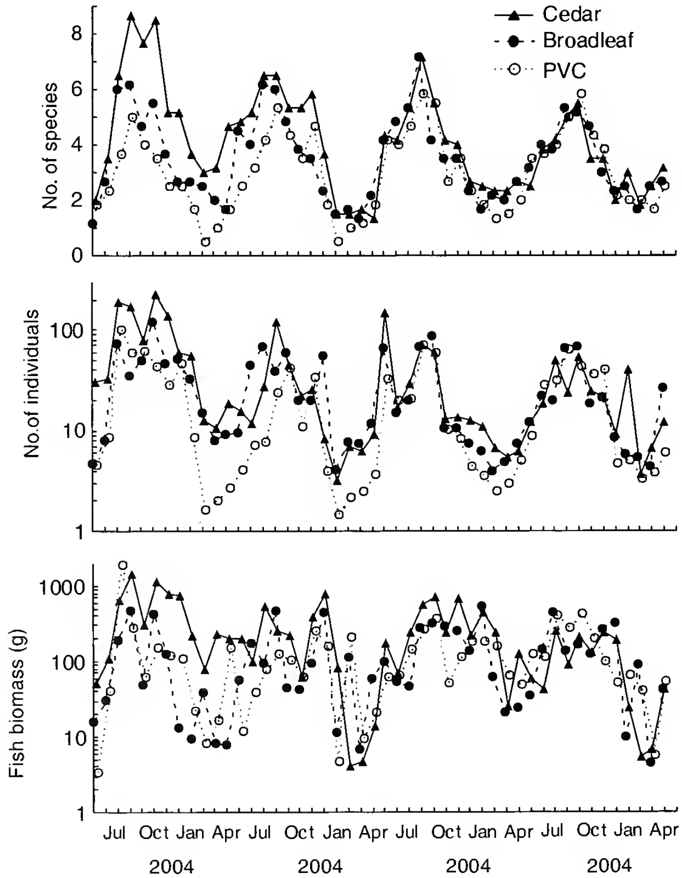

Figure 3

Species richness, fish abundance, and fish biomass associated with each type of artificial reef on each observation day between May 2004 and April 2008. Plotted data are averages of the two monthly observations carried out at each triplicate artificial reef. Note log scale for individuals and biomass plots.

Maximum, minimum, and average body length in two highly abundant and commercially important species, black rockfish and jack mackerel, are plotted for each type of artificial reef in Figure 5. Black rockfish generally had a wide range (1.5–16 cm) of body length, whereas jack mackerel had a smaller body size range (4–12 cm). This was prominent in cedar ARs, especially shortly after the deployment of the AR (Fig. 5A).

A bryozoan community was established within two to three months of deploying the cedar ARs. Other encrusting epibenthic assemblages, such as Porifera, Cnidaria, Mollusca, and Annelida, gradually formed on the broadleaf and PVC ARs after one year. The upper sections of the ARs attracted these encrusting organisms more rapidly than the lower sections. In the fourth year, some of the upper sections of the cedar and broadleaf ARs began to decay because of fouling by encrusting organisms, particularly wood boring piddock (*Martesia striata*). Crabs (*Charybdis japonica*) and sea cucumbers (*Stichopus japonicus*) were common in all types of ARs. At least four fish species, black sea bream, Temminck's surfperch (*Ditrema temmincki*), whitespotted pigmy filefish, and thread-sail filefish, were observed feeding on the encrusting organisms on and around the cedar ARs. Conger eel (*Conger myriaster*), two species of groupers, and large individuals of bambooleaf wrasse resided inside the PVC pipes. Some fish, such as thread-sail filefish and redfin velvetfish (*Paracentropogon rubripinnis*), overwintered, showing minimal movement in the cedar ARs through the winter.

Fish assemblages in the adjacent habitat

Visual censuses of the areas adjacent to the ARs revealed that both fish species richness and abundance showed clear seasonal changes corresponding to variations in sea bottom water temperature (Fig. 6). A total of 73,922 fish individuals from 90 species were recorded from 23 May 2002 to 8 May 2008 in transects 1–3. There was no significant change in fish species richness or abundance along any of the three transects after the deployment of ARs ($P>0.5$, ANCOVA; Table 3). Species-to-species analysis revealed that although there were several cases of increases or decreases in abundance after deployment, there was no evidence of a systematic decrease in species richness along transect 1, in which one species decreased and four species increased after the deployment (see far-right column in Table 2). The average (±SE) number of individuals in the entire census area of the adjacent habitat was 171 ±12.6 per 400 m^2.

Table 2

Families and species of fish found on the three types of artificial reefs, as well as the mean body length, size range, frequency of occurrence (no. of sightings from the 3 replicates x 96 bimonthly observations) and mean number of specimens observed. Different letters represent significant differences among artificial reef types ($P<0.01$, Tukey's HSD test). An increase or decrease in the number of individuals in the adjacent habitat is noted under the heading "Transects"; for example, "–2" represents a significant decrease in the transect 2 ($P<0.01$, ANCOVA). Only species which were observed three times or more are included in the table.

		Body length (cm)		Frequency			No. of individuals, mean ±SE			
Family	Species name	Mean	Range	Cedar	Broadleaf	PVC	Cedar	Broadleaf	PVC	Transects
Engraulidae	*Engraulis japonicus*	6.0	3–7	2	2	0	2.4 ±1.4	1.7±1.2		
Plotosidae	*Plotosus lineatus*	7.2	4–20	4	6	3	3.1 ±1.6	3.5±1.5	2.3 ±1.4	
Scorpaenidae	*Sebastiscus marmoratus*	11.8	5–18	8	3	5	0.031 ±0.010	0.010 ±0.006	0.017 ±0.0077	
	Sebastes joyneri	3.6	3–7	2	5	0	0.014 ±0.11	0.066 ±0.044		
	Sebastes thompsoni	3.4	2–8	8	12	10	0.35 ±0.22	0.20 ±0.077	0.48 ±0.26	
	Sebastes inermis	5.2	1.5–16	167	104	104	6.8 ±0.99^{a}	3.7 ±0.48^{b}	2.2 ±0.33^{b}	
Synanceiidae	*Paracentropogon rubripinnis*	4.8	3–7	21	29	14	0.087 ±0.019	0.14 ±0.028	0.063 ±0.015	2–
Hexagrammidae	*Hexagrammos agrammus*	11.5	9–14	4	0	0	0.017 ±0.0092			
	Hexagrammos otakii	12.8	12–16	2	5	1	0.0069 ±0.0049	0.017 ±0.0077	0.0035 ±0.0035	
Cottidae	*Furcina ishikawae*	3.7	3–4	2	1	0	0.0069 ±0.0049	0.0035 ±0.0035		
	Pseudoblennius cottoidae	6.3	3–12	62	46	35	0.31 ±0.042^{a}	0.19 ±0.028^{ab}	0.16 ±0.028^{b}	
Serranidae	*Epinephelus akaara*	14.1	10–19	4	2	12	0.014 ±0.0069^{b}	0.0069 ±0.0049^{b}	0.045 ±0.013^{a}	
	Epinephelus awoara	9.1	4–15	6	2	11	0.021 ±0.0084	0.0069 ±0.0049	0.038 ±0.011	
Apogonidae	*Apogon semilineatus*	4.3	2–6	4	3	20	0.049 ±0.036^{b}	0.017 ±0.010^{b}	1.5 ±0.38^{a}	
Carangidae	*Trachurus japonicus*	6.7	4–12	38	38	41	9.4 ±2.3	5.4 ±1.5	6.3 ±1.2	2–
Lutjanidae	*Lutjanus russellii*	6.0	5–8	1	3	1	0.0035 ±0.0035	0.10 ±0.0060	0.0035 ±0.0035	
	Lutjanus ophuysenii	4.7	3–7	8	11	7	0.069 ±0.038	0.27 ±0.12	0.10 ±0.047	
Haemulidae	*Parapristipoma trilineatum*	3.9	3–5	2	4	7	0.021 ±0.018	0.17 ±0.11	0.087 ±0.035	
Sparidae	*Acanthopagrus schlegelii*	28.6	6–40	36	26	14	0.19 ±0.037^{a}	0.16 ±0.032^{ab}	0.059 ±0.037^{b}	
	Pagrus major	6.5	2–14	18	15	4	0.080 ±0.019	0.080 ±0.025	0.014 ±0.0069	1+ 2+
Pentacerotidae	*Evistias acutirostris*	35.0		2	0	1	0.0069 ±0.0049		0.0035 ±0.0035	
Cheilodactylidae	*Goniistius quadricornis*	6.3	3–12	6	2	2	0.024 ±0.010	0.0069 ±0.0049	0.0069 ±0.0049	
Embiotocidae	*Ditrema temmincki*	7.5	3–16	37	18	20	0.15 ±0.024	0.080 ±0.019	0.094 ±0.022	
Pomacentridae	*Chromis notata*	3.7	3–4	2	1	0	0.0069 ±0.0049	0.0035 ±0.0035		
Oplegnathidae	*Oplegnathus fasciatus*	5.9	3–8	4	2	2	0.23 ±0.21	0.0069 ±0.0049	0.11 ±0.10	
Girellidae	*Girella punctata*	9.8	6–15	4	1	4	0.080 ±0.070	0.010 ±0.010	0.045 ±0.026	
Labridae	*Choerodon azurio*	18.4	16–22	2	1	2	0.0069 ±0.0049	0.0035 ±0.0035	0.0069 ±0.0049	
	Pseudolabrus sieboldi	9.7	1–25	135	110	141	0.99 ±0.089^{a}	0.62 ±0.089^{b}	0.94 ±0.060^{a}	
	Halichoeres poecilopterus	13.7	8–20	11	6	2	0.049 ±0.016	0.024 ±0.010	0.0069 ±0.0049	3–
	Halichoeres tenuispinnis	11.6	5–15	5	3	1	0.024 ±0.011	0.014 ±0.0085	0.0035 ±0.0035	
Stichaeidae	*Dictyosoma burgeri*	16.0	14–18	0	3	0		0.010 ±0.0060		
Blenniidae	*Parablennius yatabei*	3.9	2–6	4	6	0	0.024 ±0.010	0.024 ±0.010		
	Petroscirtes breviceps	5.3	1–8	16	16	12	0.080 ±0.022	0.076 ±0.028	0.066 ±0.023	

Continued

Table 2 (continued)

Family	Species name	Body length (cm)		Frequency			No. of individuals, mean ±SE			Transects
		Mean	Range	Cedar	Broadleaf	PVC	Cedar	Broadleaf	PVC	
Gobiidae	*Chaenogobius gulosus*	3.3	2–4	2	1	1	1.5 ±1.4	0.010 ±0.010	0.0069 ±0.0049	
	Pterogobius zonoleucus	3.8	3–5	4	4	0	1.3 ±1.1	0.53 ±0.39		
	Istigobius hoshinonis	5.8	6–9	2	10	2	0.0069 ±0.0049^b	0.038 ±0.012^a	0.0069 ±0.0049^b	
	Istigobius campbelli	5.4	2–7	3	3	3	0.010 ±0.0060	0.010 ±0.0060	0.014 ±0.0085	
	Acentrogobius pflaumii	3.0	1–5	2	4	3	0.010 ±0.0060	0.014 ±0.0069	0.010 ±0.0060	1–
	Tridentiger trigonocephalus	2.8	1–5	151	175	105	2.9 ±0.35^b	5.1 ±0.51^a	2.1 ±0.29^b	1+ 2+
Sphyraenidae	*Sphyraena pinguis*	13.9	10–18	4	0	4	0.80 ±0.54		0.45±0.25	
Monacanthidae	*Rudarius ercodes*	2.4	1–5	183	157	124	8.6 ±10.98^a	5.1±0.76^b	2.8 ±0.53^b	1+2+
	Thamnaconus modestus	6.2	5–11	5	6	2	0.017 ±0.0077	0.056 ±0.028	0.014 ±0.011	
	Stephanolepis cirrhifer	5.7	2–18	30	25	20	0.27 ±0.063^a	0.19 ±0.044^{ab}	0.090 ±0.021^b	
Tetradontidae	*Takifugu poecilonotus*	9.7	6–20	56	32	24	0.26 ±0.035^a	0.15 ±0.025^{ab}	0.12 ±0.023^b	1+ 3+
	Takifugu niphobles	6.3	3–8	17	6	8	0.16 ±0.11	0.039 ±0.016	0.049 ±0.021	

Discussion

The greater effectiveness of cedar ARs

We found that ARs made from logs of cedar trees had a higher fish species richness and abundance than those made of broadleaf trees or PVC pipes. The greater effectiveness of the cedar ARs can be attributed to the direct or indirect effects of cedar wood as an AR material. Qualitative observations support the latter because we observed some fish feeding on encrusting organisms on the cedar ARs. Cedar emits volatile compounds that repel terrestrial invertebrates to protect the living tree (Morisawa et al., 2002), but such chemicals might not be effective as repellants in seawater, making it a suitable habitat for fouling marine organisms. The rapid growth of cedar trees results in relatively soft tissues that can further make the wood a suitable substrate for fouling organisms. A comparison of the abundance of epibenthic assemblages between cedar and broadleaf logs will be required to confirm this hypothesis.

Redspotted grouper was significantly more abundant in PVC ARs than in the other two types of ARs. The body length of this species was an average of 14 cm and ranged from 10 to 19 cm (Table 2), and the inner diameter of the PVC pipes was 11 cm. ARs with holes are expected to host more fish (Kellison and Sedberry, 1998), especially large predators (Hixon and Beets, 1989). Indeed, PVC pipes, because of their size, provided a suitable shelter for redspotted groupers. Yellowspotted grouper (*E. awoara*), conger eel, and some large individuals of bambooleaf wrasse also used the cavities of the PVC pipes.

Two species of goby were more abundant in the broadleaf ARs than in the other two ARs. Most of these gobies ranged from 1 to 5 cm. Predation pressure by the abundant sunrise sculpin and black rockfish in the cedar ARs, and groupers in the PVC ARs, may have reduced the survival of gobies in these two types of ARs, resulting in the relatively higher abundance of gobies in the broadleaf ARs.

Black rockfish associated with cedar ARs ranged from 1.5 to 16 cm SL. Black rockfish is a viviparous fish and matures at 12 cm BL in 1–2 years after birth, and 1.5 cm and 16 cm SL individuals represent 1.5-month and 4–5 year-old individuals, respectively (Hisada et al., 2000). Whitespotted pigmy filefish associated with cedar ARs ranged from 1 to 5 cm SL. Whitespotted pigmy filefish mature at 3 cm SL (Ishida and Tanaka, 1983). Therefore these species use ARs as settlement sites, nurseries, and adult habitats. Jack mackerel associated with ARs ranged from 4 to 12 cm SL. Jack mackerel mature at 14 cm SL (Ochiai et al., 1983) and attain 4 cm in 2 months (Xie et al., 2005). Therefore they use ARs mainly as nursery habitat and are loosely associated with ARs. This finding is in agreement with that of Rooker et al. (1997) who reported that some midwater pelagic fishes, such as carangids and scombrids, were transient members of the AR fish assemblages. Considering that there are both pelagic predators, such

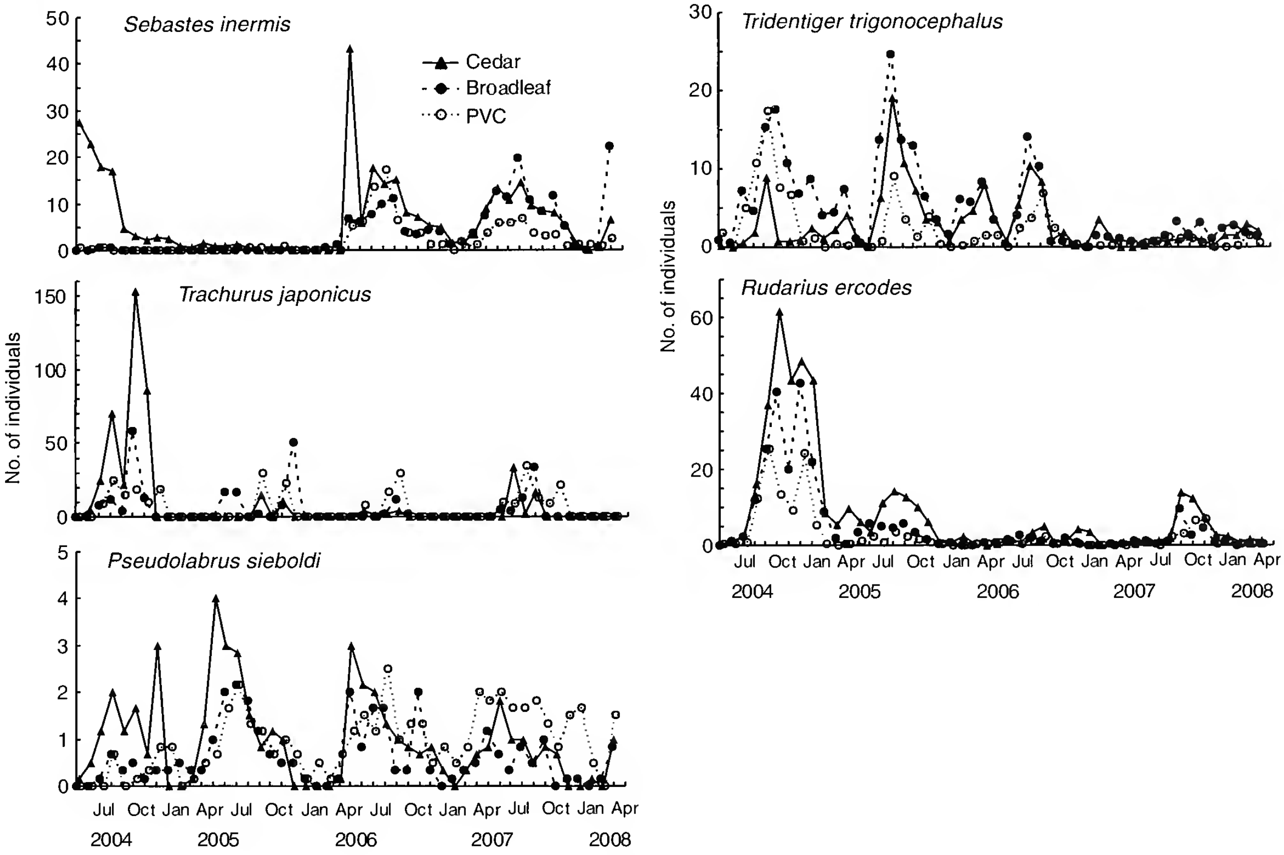

Figure 4

The monthly average of individuals of black rockfish (*Sebastes inermis*), jack mackerel (*Trachurus japonicus*), bambooleaf wrasse (*Pseudolabrus sieboldi*), chameleon goby (*Tridentiger trigonocephalus*), and whitespotted pigmy filefish (*Rudarius ercodes*) associated with each type of artificial reef installed off Maizuru, Kyoto, in 2004.

as Japanese seabass (*Lateolabrax japonicus*), and benthic predators, such as Japanese flounder (*Paralichthys olivaceus*), in this area (Masuda, 2008), these ARs may well be used as refuges from predators.

Because the size of ARs was 1.5×1.5 m and fish were counted within a distance of 1 m, the survey area represented about 10 m^2 for each AR. The density of fish associated with the AR was estimated as 4.07, 2.79, and 2.03 fish per m^2 in and around the cedar, broadleaf, and PVC ARs, respectively (Table 1). Santos et al. (2005) studied fish assemblages associated with ARs made of concrete blocks located at a similar latitude but deeper depth (17–22 m) in south Portugal (37°00′N lat., 7°45′ and 8°00′E long.), and estimated the mean fish density as 2.01 ±0.74 fish per m^2 and fish biomass as 123.6 ±77.4 g per m^2. Fish density on our cedar ARs was about twice as much but the biomass was much less than the value reported by Santos et al. This finding was probably the result of the cedar ARs hosting more recruited juveniles than adults.

Table 3

The number of species and number of individuals of fish recorded during observations along transects 1, 2, and 3 before and after the deployment of the artificial reefs, expressed as the mean ±standard error (n=48 and 96 observations for before and after deployment, respectively).

	Transect 1	Transect 2	Transect 3
No. of species			
Before deployment	9.69 ±0.61	9.67 ±0.60	8.88 ±0.62
After deployment	9.40 ±0.43	9.44 ±0.47	8.40 ±0.42
No. of individuals			
Before deployment	116.9 ±21.5	237.6 ±44.6	178.0 ±37.4
After deployment	165.7 ±22.7	225.9 ±34.8	171.1 ±28.9

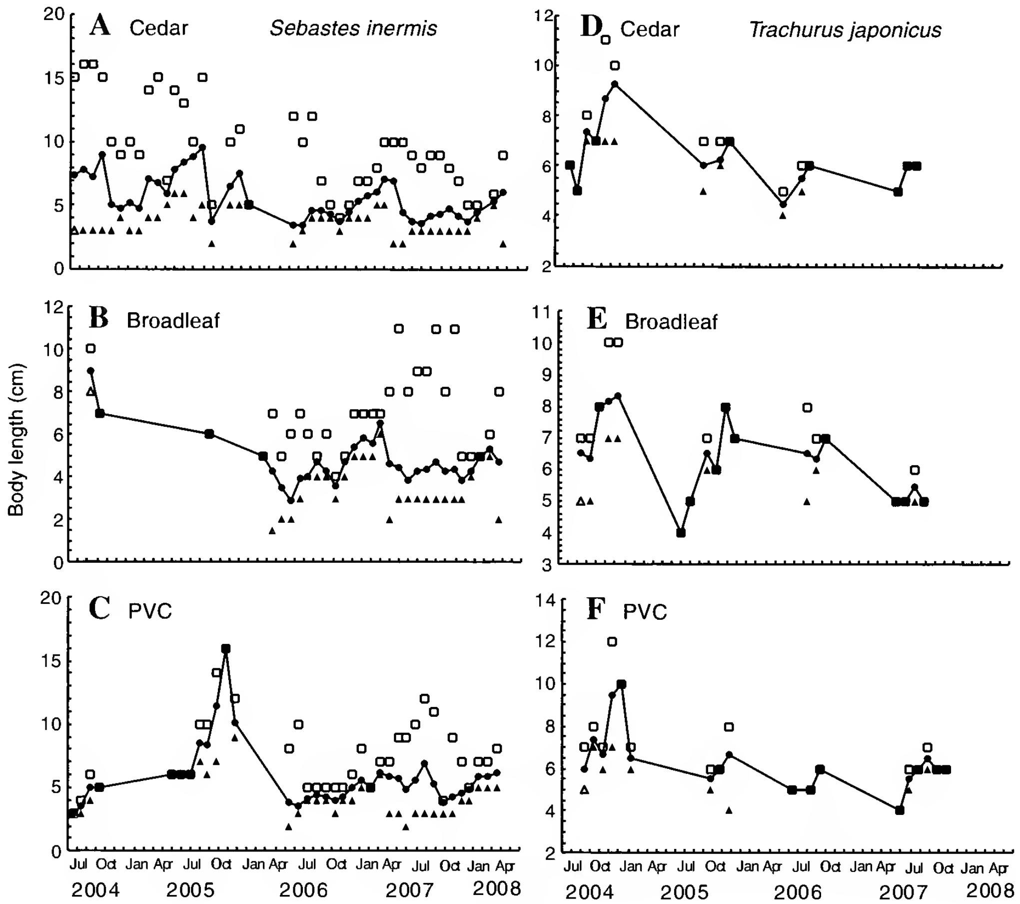

Figure 5

Monthly maximum (rectangles), minimum (triangles), and average (circles) body length of black rockfish (*Sebastes inermis*) found associated with (**A**) cedar, (**B**) broadleaf, and (**C**) PVC artificial reefs, and those of jack mackerel (*Trachurus japonicus*) found associated with (**D**) cedar, (**E**) broadleaf, and (**F**) PVC artificial reefs.

The cedar ARs hosted fish assemblages within the first two to three months of deployment. These recruits may have come from the adjacent coastal habitat or from offshore. Rapid colonization of ARs was also reported by Bohnsack et al. (1994) who observed that fish species, number of individuals, and biomass reached peak levels within two months of deploying concrete ARs in Florida.

There was only one species, *Acentrogobius pflaumii*, that decreased in abundance in transect 1 after the deployment of ARs. This goby is the fifth most frequently observed fish in the adjacent natural reef (Masuda, 2008), but relatively few were associated with ARs. Therefore it is unlikely that the attraction to ARs induced the decline in the population along transect 1. The relative stability of fish species and abundance observed among the three transects supports the concept of an inshore migration and is in agreement with data of Connell (1997) who found that the number of recruits did not differ between ARs located close to and far from a natural reef. Sánchez-Jerez and Ramos-Esplá (2000) also confirmed that antitrawling reefs deployed in a seagrass habitat had little effect on seagrass fish assemblages in the surrounding area. We therefore conclude that the three types of ARs deployed in this study provided additional habitat for young fish without any significant depletion of numbers in the existing fish community.

The average number of fish in the adjacent habitat was 171 individuals per 400 m^2, or 0.43 individuals per m^2. Fish density on the cedar reef was thus 10 times larger than that of the adjacent area. Bohnsack et al. (1991) reviewed experimental studies, where fish densities at natural reefs were compared with those at artificial reefs, and found that in some cases the latter can host densities of more than 10 times that of the former. Therefore, our results of fish density on cedar ARs are within the range of previously reported ARs.

Deployment of wooden ARs as a tool for ecosystem-based fishery management

The major anthropogenic impacts on coastal ecosystems include overfishing, loss of physical complexity induced by construction or trawling, and eutrophication induced by water discharge. ARs made of cedar and other materials have the potential to attenuate at least some of these problems. ARs are useful in that they preclude trawling, protect juveniles in nursery grounds, and provide fishing sites for artisanal fishermen (Polovina, 1991). Our study site had also been a trawl fishing ground for bivalves and sea cucumbers, but fishermen could not trawl at our ARs. The prevention of trawling resulted in the accumulation of relatively large individuals of sea cucumber in our ARs (R. Masuda, unpubl. data). Habitat complexity, such as vertical relief and holes, can be a positive factor for the survival of juvenile fish. For instance, Gorham and Alevizon (1989) showed that the attachment of polypropylene rope to ARs significantly increases the abundance of juvenile fish. Wooden ARs not only provide vertical relief but also provide a porous substrate for boring and attachment by encrusting organisms, such as boring sponges, oysters, and wood boring piddock. Some demersal fishes, such as black rockfish, wrasses, and gobies might well use these encrusting organisms for both refuge and as prey.

Most of the encrusting organisms on ARs are plankton feeders that can use a wide size range of phytoplankton and zooplankton. For example, a single oyster filters several liters of sea water per day and produces pseudofeces that contain about half of the organic content of that trapped on the gills (Deslous-Paoli et al., 1992). Most juvenile and young demersal fish feed on benthic organisms in addition to relatively large zooplankton. Therefore, encrusting organisms on ARs can transform phytoplankton and microzooplankton to a usable energy source for fishes. Fabi et al. (2006) demonstrated that ARs provide the main food source (e.g., encrusted organisms and crustaceans) for the three major fish species (*Sciaena umbra*, *Diplodus annularis*, and *Lithognathus mormyrus*) they studied. Furthermore, improved water clarity due to the filtering function of the encrusting organisms is likely to result in the better growth of primary producers, such as macroalgae. The use of fish reefs as biofilters for nutrient removal has also been proposed by Seaman and Jensen (2000).

The efficacy of wooden ARs is of a short duration (up to 3–5 years) compared to those made of concrete, which can last decades (Yabe, 1995). However, fishermen have observed that wooden ARs attract fish sooner than other types of AR. Although wooden ARs biodegrade sooner than concrete ARs, from an ecological point of view of providing immediate refuge, habitat, and a source of food, they have long-term effects on the marine environment. Simple wooden ARs that combine logs and concrete blocks sink easily in a muddy substrate, and their life as an effective AR can be as short as one year (R. Masuda, personal observ.). The shape of wooden ARs presented in this article, with a double-cross formation (Fig. 1), provides an open and stable vertical relief that can attract more fish recruits. This formation can also act as a stable substrate for encrusting organisms that can function as powerful biofilters, and has a longer durability than other wooden constructs.

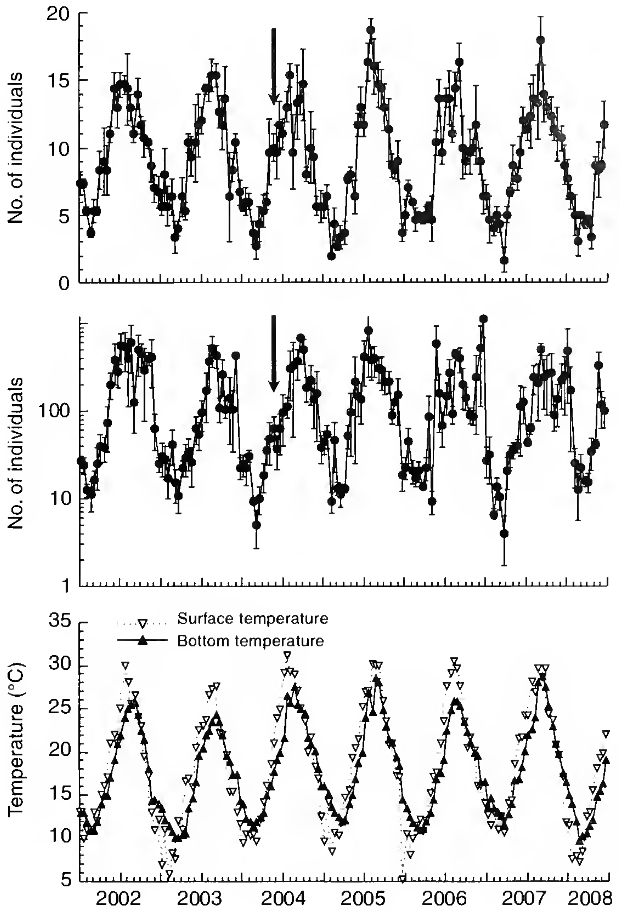

Figure 6

Seasonal changes in the mean (±standard error) number of fish species and individuals per transect in the area immediately adjacent to the artificial reefs, and the surface and bottom water temperatures measured in those areas during the surveys from January 2002 to June 2008, at Nagahama, Maizuru, Japan. Vertical arrows represent the date (21 May 2004) of artificial reef deployment.

The recruitment of reef fishes is often limited by the availability of suitable nearshore nursery habitats, which tend to be vulnerable to anthropogenic impacts. The decrease of reef fish populations is therefore partly attributable to the loss of nursery habitats, such as natural rocky reefs and seagrass beds. The deployment of wooden ARs may provide an opportunity to mitigate this trend of decline in nursery quality and because they are highly biodegradable, the risks of unexpected negative impacts on the environment are minimal. Stock enhancement, defined as the release of cultured juveniles into wild populations to augment harvest, has been used as a strategy to reconstruct depleted fisheries resources (Bell et al., 2008). We suggest that the release of reef-associating fish juveniles, such as black rockfish, combined with the deployment of wooden ARs would be an efficient approach for the recovery of depleted coastal fisheries.

A major problem of deploying ARs is that they attract fishermen as well as fishes. There is always the possibility that fishermen will catch more fish than the increase of production because fish attracted to ARs are generally more easily exploitable than those spread over natural reefs (Powers et al., 2003). Indeed, we often observed local anglers fishing at our experimental reefs. Therefore, a management strategy is critically important in controlling the harvesting pressure at AR sites (Pickering and Whitmarsh, 1997). As our long-term goal is to improve the productivity of local inshore fishing grounds, we would suggest that part of the areas to be enhanced should have ARs distributed within them and be managed as marine protected areas.

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Abstract—The Pacific sardine (*Sardinops sagax*) is distributed along the west coast of North America from Baja California to British Columbia. This article presents estimates of biomass, spawning biomass, and related biological parameters based on four trawl-ichthyoplankton surveys conducted during July 2003–March 2005 off Oregon and Washington. The trawl-based biomass estimates, serving as relative abundance, were 198,600 t (coefficient of variation [CV]=0.51) in July 2003, 20,100 t (0.8) in March 2004, 77,900 t (0.34) in July 2004, and 30,100 t (0.72) in March 2005 over an area close to 200,000 km^2. The biomass estimates, high in July and low in March, are a strong indication of migration in and out of this area. Sardine spawn in July off the Pacific Northwest (PNW) coast and none of the sampled fish had spawned in March. The estimated spawning biomass for July 2003 and July 2004 was 39,184 t (0.57) and 84,120 t (0.93), respectively. The average active female sardine in the PNW spawned every 20–40 days compared to every 6–8 days off California. The spawning habitat was located in the southeastern area off the PNW coast, a shift from the northwest area off the PNW coast in the 1990s. Egg production in off the PNW for 2003–04 was lower than that off California and that in the 1990s. Because the biomass of Pacific sardine off the PNW appears to be supported heavily by migratory fish from California, the sustainability of the local PNW population relies on the stability of the population off California, and on local oceanographic conditions for local residence.

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Biomass and reproduction of Pacific sardine (*Sardinops sagax*) off the Pacific northwestern United States, 2003–2005

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Pacific sardine (*Sardinops sagax*; hereafter "sardine") are distributed widely off the west coast of North America from Baja California, Mexico, to British Columbia, Canada; the majority of the population is located off California (Felin, 1954; Murphy, 1966; Emmett et al., 2005; McFarlane et al., 2005; Smith, 2005). Tagging studies have shown that sardine migrate along the west coast (Janssen, 1938; Clark and Janssen, 1945). The sardine population reached a peak in the early 1930s at 3.5 million metric tons (t) and declined rapidly in the mid-1950s (Marr, 1950). The sardine fishery off California and British Columbia dates from 1916 (Fig. 1). Pacific sardine was one of the economically important species off California and British Columbia in the 1930s when a fishery began off Oregon and Washington (the Pacific Northwest: PNW). The PNW catch peaked at nearly 50,000 t in 1938 (Marr, 1950; Mosher and Eckles, 1954; Murphy, 1966). In the 1960s, however, a moratorium on sardine fishing was established in U.S. waters because of low catches (Murphy, 1966; MacCall, 1976). In the mid 1980s, sardine became common as bycatch in fisheries off Baja California and California state (Wolf, 1992; Deriso et al., 1996) and reappeared from Oregon to British Columbia in 1992 (Emmett et al., 2005; McFarlane et al., 2005), apparently in response to the 1992–93 El Niño event. The sardine population now supports a relatively large fishery with annual catches over 50,000 t in recent years (Fig. 1). Sardine also serve as important food for tuna, salmon, marlin, mackerel, sharks, and some groundfish species, as well as many seabirds, seals, sea lions, dolphins, and whales (Snodgrass and Lowry, personal commun.[1]) (Preti et al., 2001, 2004; Emmett et al., 2005). The reappearance of sardine populations in the north California Current ecosystem adds another forage base for predators and an emerging resource of consumer interest to the ecosystem.

Pacific sardine off the PNW are considered to be a part of the northern subpopulation, the majority of which is distributed off the western United States and Canada (Smith, 2005), as determined from historical tagging studies (Clark and Janssen, 1945), size at age, and other biological characters. Historical tagging studies indicated that some large sardine migrate from California to the PNW in late spring and early summer to feed, and that the majority of the large sardine off the PNW move south to California in the winter to spawn in the spring (Clark and Janssen, 1945). The major spawning area of this northern subpopulation was believed to be located off southern California before the 1960s (Ahlstrom, 1948; Marr, 1960; Smith, 2005). Spawning also may have occurred in the PNW because young fish were caught by commercial boats in Canadian waters in 1940 (Hart, 1943). However,

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[1] Snodgrass, Owyn. 2009. Southwest Fisheries Science Center, La Jolla, CA. Lowry, Mark. 2009. Southwest Fisheries Science Center, La Jolla, CA.

the importance of the PNW as a spawning area has not been studied. After the resurgence of Pacific sardine off California, ichthyoplankton and fishery-independent trawl surveys have been conducted off California to assess the biological characteristics of the sardine population since the mid 1980s, when the estimated sardine biomass approached 20,000 t (Wolf, 1992; Lo et al., 2005). Beginning in the mid 1990s, sardine abundance, distribution, and ecological relationships off the PNW and Canada were analyzed with data from salmon surface-rope trawl surveys off the PNW and trawl surveys off Vancouver Island, Canada (Bentley et al., 1996; Emmett et al., 2005; McFarlane et. al., 2005); however, very few of those surveys were designed specifically to assess the biological characteristics of Pacific sardine.

Four trawl surveys off the PNW were conducted in July 2003, March and July 2004, and March 2005 to provide fishery-independent measures of biological characteristics of sardine in this area, and to answer the following questions: 1) Do sardine migrate between the PNW and California? 2) To what extent does Pacific sardine spawning in the PNW depend on the sardine population off California? and 3) How much does the Pacific sardine egg production in the PNW contribute to that of the whole population? To answer these questions, we estimated spring and summer biomasses with length distributions to serve as signals of migration; the location and spatial extent of spawning habitat to examine the following: the effect of the reduction of the spawning area in the PNW to the local population; daily egg production and its contribution to the total egg production; adult reproductive parameters to estimate rates of spawning, fecundity and maturity; and spawning biomass. These measurements were compared with available PNW measurements from the mid-1990s and those off California in the same time period, to facilitate our understanding of the population dynamics of the Pacific sardine off the northern west coast of the North American continent, and to better manage the entire population.

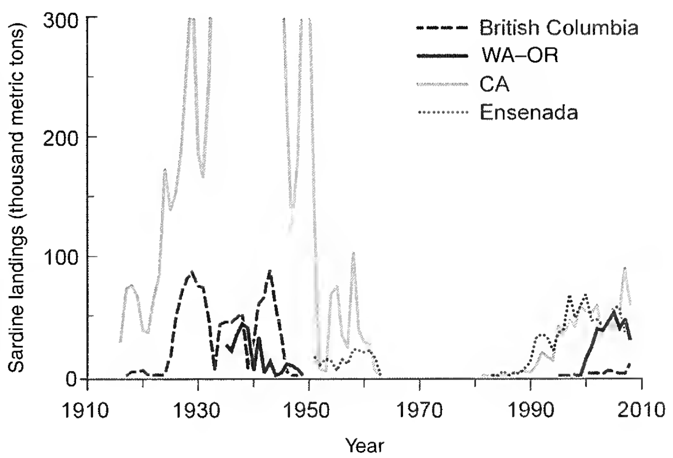

Figure 1

Commercial landings of Pacific sardine (*Sardinops sagax*) in British Columbia, Canada, Washington, and Oregon, and California; and Ensenada, Mexico, from 1916 through 2008. *Y*-axis is truncated because during 1933–45 and 1950–51 California landings exceeded 300,000 t with a peak in 1936 of 791,334 t.

Materials and methods

Survey

In order to obtain unbiased estimates of the biological characteristics of Pacific sardine off the PNW, the Fisheries Resources Division of the Southwest Fisheries Science Center, conducted four surveys in July 2003, March and July 2004, and March 2005 aboard the FV *Frosti*. Multiple gear types were used: a surface trawl to collect adult samples, the CalVET plankton net (California Cooperative Oceanic Fisheries Investigation vertical-egg-tow net; Smith et al., 1985), and the continuous underway fish egg sampler (CUFES; Checkley et al., 1997) to collect ichthyoplankton samples and record hydroacoustics. The survey region encompassed the area of the northeast Pacific Ocean from 42° to 48°N latitude and from inshore out to 128°W longitude.

The basic survey pattern comprised seven transect lines oriented on the parallels at a spacing of 60 nautical miles (111 km). Stations were spaced at 30 nautical miles (55.5 km) along each transect measured from the offshore station. Forty-two predetermined stations were sampled by trawl and CalVET tow during each survey. For the July 2003 survey, the primary goal was to estimate the spawning biomass of Pacific sardine. In the offshore area, few trawls were undertaken because both acoustics and CUFES samples showed little sign of sardine schools and eggs. The inshore sampling was discontinued close to the 100-m isobath during July 2003 to avoid net damage in shallow water. All fishing was conducted at night, when Pacific sardine are distributed in the upper 50 m of the water column and oceanographic conditions at depths greater than 50 m would have little influence on the spatial and vertical distributions of sardine schools. Moreover, within 60 km from the shore, the densities of fish were not related to the distance from shore (Emmett et al., 2005). Therefore we expected little bias introduced from sampling along the 100-m isobath. With more experience, we found that we could tow the net at a shallower depth than initially expected, and during subsequent surveys we occasionally fished inshore at shallower depths (see below, Figs. 2–5). For the remaining three surveys, most trawls were evenly distributed along the transect line and between transect lines in the inshore area. Occasionally, trawls were made during transit between transect lines.

Both trawl and CalVET samples were collected during all four surveys and CUFES samples were collected during July surveys only (Figs. 2–5). Trawl-related

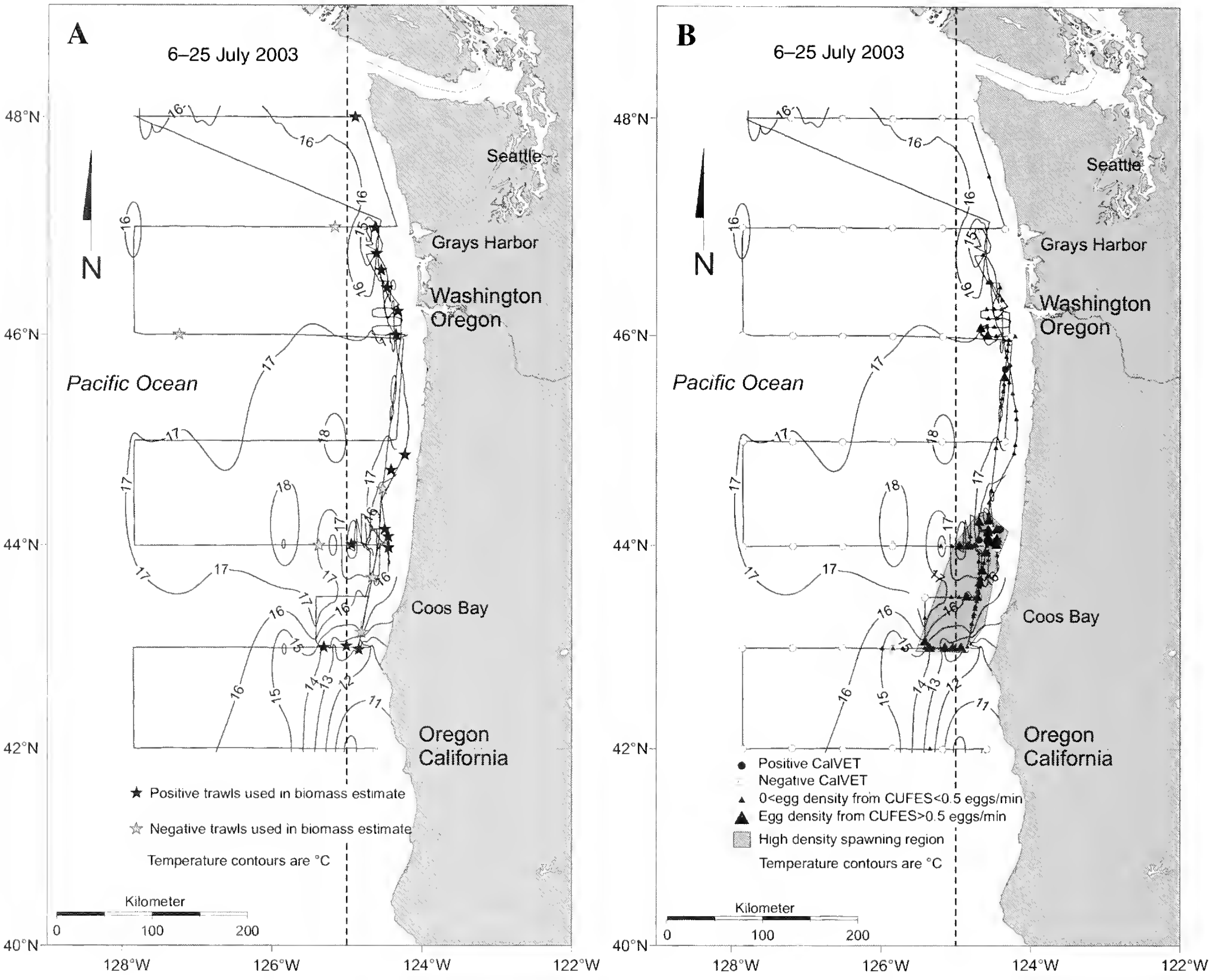

Figure 2

(**A**) Locations of trawls (stars) used for the estimation of biomass of Pacific sardine (*Sardinops sagax*), excluding added trawls in the inshore area (Table 1), and (**B**) locations of California vertical egg tows (CalVET: circles) and where continuous underway egg samples were taken (measured in eggs per minute (CUFES: triangles). Contours are sea surface temperatures (°C). The dashed vertical line is the 125°W longitude divider of the two sampling strata. The offshore shaded area in (B) is the major spawning habitat. Positive tows were those tows during which sardine were caught. Negative tows were tows when sardine were not caught.

station activities were performed between twilight and dawn, whereas CalVET and CUFES samples were collected throughout all 24 hours. At each station, a CalVET sample was collected and sea surface temperature (SST) was recorded, whereas between stations, CUFES samples and water temperature were taken at a fixed 3-m depth (Figs. 2 and 4). The CUFES data were used primarily to map the spawning area based on the density of sardine eggs.

A Nordic 264 trawl (NET Systems, Bainbridge Island, WA), with a vertical opening of 20 m, a mouth area of approximately 360 m^2, and a 7-mm codend mesh (Emmett et al., 2005), was towed to sample the upper 18–20 m of the water column. The distance traveled by each trawl was recorded and was later converted to the volume sampled. The swept area (m^2) is the volume (m^3) divided by 20 m. During the July 2003 survey, few trawls were taken in the offshore area. Additional trawls were taken inshore to collect extra samples to determine reproductive parameters in areas of sardine spawning activity identified by sardine egg densities in CUFES samples or the presence of schools as indicated by acoustic signals (Fig. 2). Similarly, during July 2004, trawls were taken in the southern spawning area off Port Orford, OR (Fig. 4), in addition to the prepositioned and between-transect trawls. Data from the added trawls were excluded in estimating the total biomass to avoid bias. For the two March surveys, all locations (fixed stations and between-transects) were trawled regardless of spawning or acoustic signals (Figs. 3 and 5). The total number of trawls for each survey was close to 50 (Table 1).

For each trawl, the total weight (kg) of the Pacific sardine catch was recorded and up to 50 Pacific sardine were randomly sampled from each trawl where sardine were caught (hereafter referred to as a "positive trawl"). Sex was determined for each fish, and standard length (SL) and weight were measured. For the female fish, the ovaries were first examined for torpedo shape and or development of visible oocytes (yolking or hydrating). When oocytes were not visible and the ovary was small, clear, and torpedo shaped, the ovary was recorded as code 1 (clearly immature). Otherwise, the additional ovarian codes 2 (intermediate), 3 (active), or 4 (hydrated) (Table 2) were used to identify *potentially* mature females—because only histological analysis can verify sardine maturity with certainty (Macewicz et al., 1996). All ovaries were removed and preserved in 10% neutral buffered formalin. If a 50-fish subsample did not have 25 potentially mature females (ovary codes 2–4), more females were sampled to attain 25 per trawl for estimation of reproductive parameters used for computing spawning biomass. Additional females were also processed to estimate batch fecundity, but were not included in the original random subsample for length distributions. We also obtained length distributions based on data from commercial purse seine catches off the PNW in the summer seasons and from a test purse seine set in March 2005.

Seasonal biomass

A swept-area method was used to estimate the total biomass of Pacific sardine in summer and spring based on July and March trawl data, respectively. Because the efficiency of the trawl catch has not been evaluated, the biomass estimates must be considered as relative and minimum

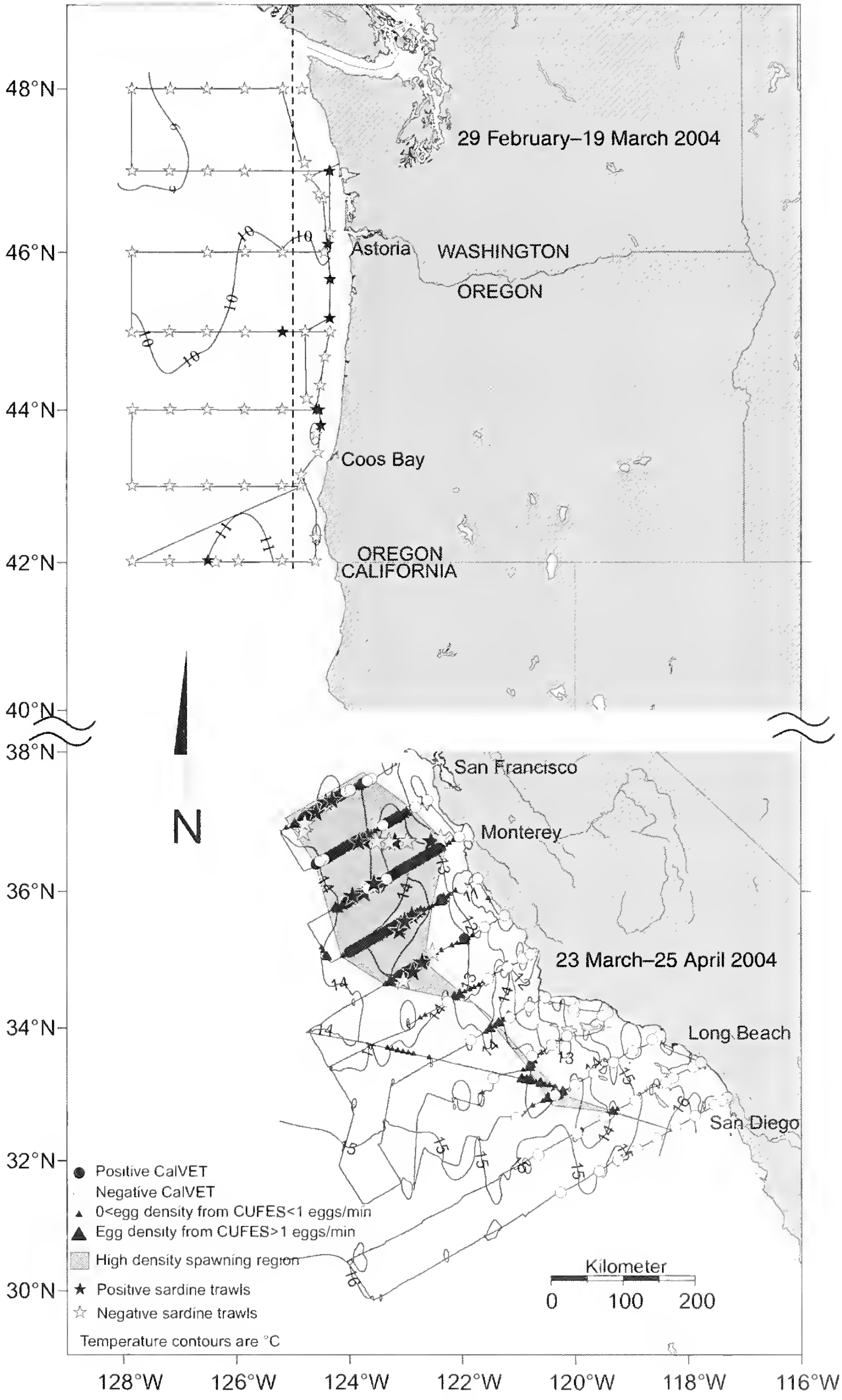

Figure 3

Locations of trawl (stars) and California vertical egg tows (CalVET; circles), for 2004 March ichthyoplankton-trawl survey off the Pacific Northwest (top map), and locations of trawls, CalVET tows (circles), and continuous underway egg sampling (CUFES: triangles) for the March–April 2004 California Cooperative Oceanic Fisheries Investigations (CalCOFI) daily egg production survey (bottom map). Solid symbols indicate that Pacific sardine (*Sardinops sagax*) were captured in the sample at that site. Contours are sea surface temperatures (°C). The dashed vertical line at 125°W longitude (seen in top map) is the divider of the two sampling strata. The shaded area on the bottom is the identified spawning habitat.

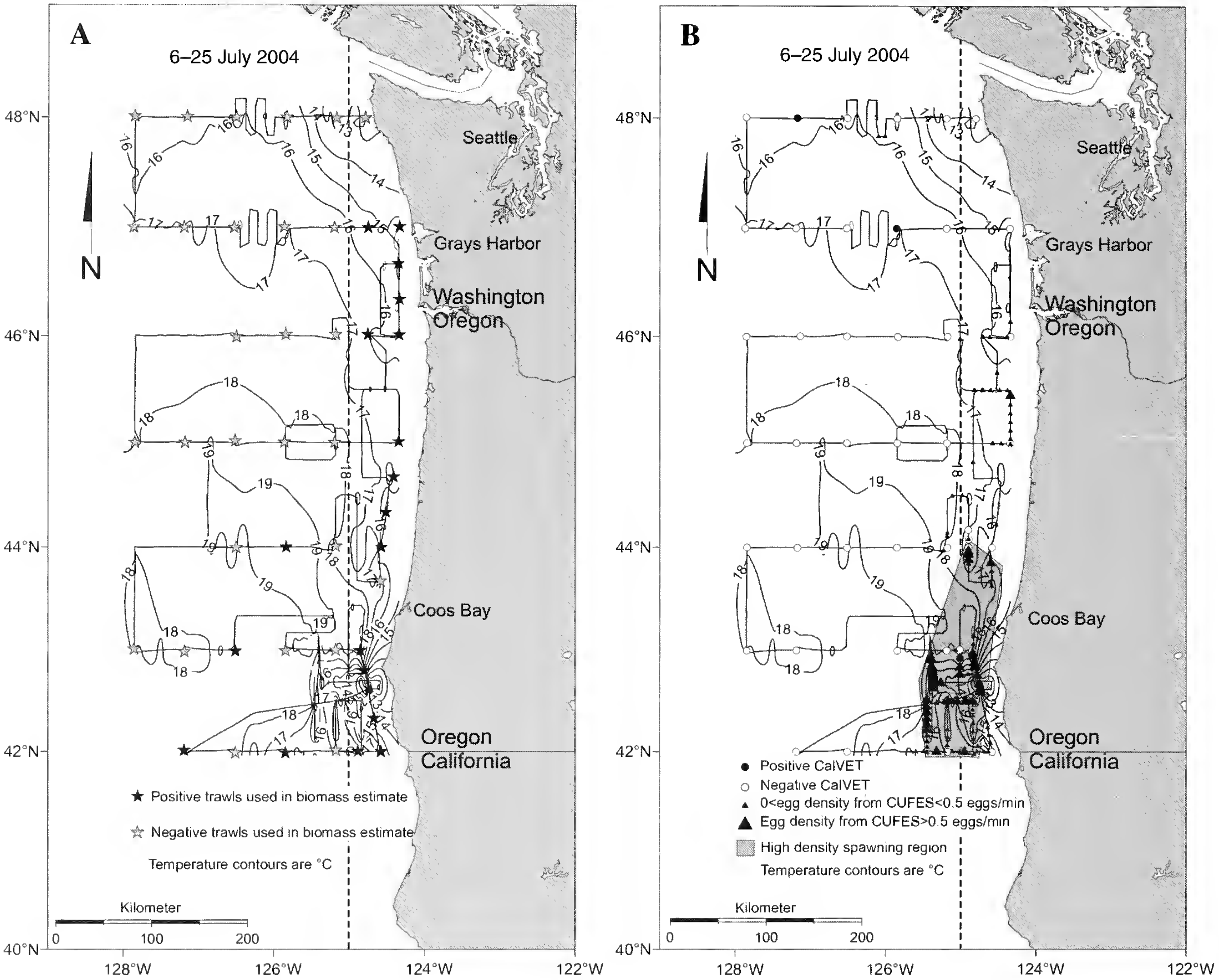

Figure 4

(**A**) Locations of trawls (stars) used for biomass estimation of Pacific sardine (*Sardinops sagax*), excluding added trawls in the inshore area (Table 1), and (**B**) California vertical egg tows (CalVET: circles) and continuous underway egg sampling in eggs/minute (CUFES: triangles) for 2004 July trawl-ichthyoplankton survey off the Pacific Northwest. Contours are sea surface temperatures (°C). The dashed vertical line is the 125°W longitude divider of the two sampling strata. The shaded area is the major spawning habitat. Positive tows were those tows during which sardine were caught. Negative tows were tows when sardine were not caught.

abundances. A stratified sampling design was used to estimate biomass and spawning biomass, because more stations were assigned close to the shore than offshore. Otherwise, estimates would be biased toward the inshore area (Holt and Smith, 1979). The survey area was divided into an inshore area (stratum 1) and an offshore area (stratum 2) with 125°W longitude as the dividing line. For the July 2003 survey, we excluded the nonpredetermined trawls (i.e., those trawls locations of which were not determined before the survey) taken in the vicinity of positive trawls to prevent an overestimate of the total biomass. The catch for each tow was expressed as kg/m^2 (=catch [kg]/swept area[m^2]=catch [kg]/volume of water [m^3]/depth 20 m), where the volume of water filtered was computed as the distance covered by each tow multiplied by the area of the vertical trawl mouth opening of approximately 360 m^2 (with 20 m as diameter). We estimated relative total biomass (B) and its standard error (SE) for each survey as follows:

$$\hat{B}=\sum_i \bar{X}_i(A_i 10^6)/1000, \qquad (1)$$

$$SE(\hat{B})=\Big(\sum_i \Big(\mathrm{var}(\bar{X}_i)\,(A_i 10^6)^2\Big)\Big)^{1/2}/1000 \qquad (2)$$

where $\hat{B}$ = the estimate of the total biomass (t);
$\bar{X}_i$ = the mean catch (kg/m^2); and

A_i = the area (km^2) in stratum i, i=1 (inshore) and 2 (offshore).

Note: the coefficient of variance (CV) of the estimate is $CV(\hat{B}) = SE(\hat{B})/\hat{B}$. Bootstrap simulation was used to estimate the bias of the estimate (Eq. 1), and the bias-corrected estimate ($\hat{B}_c$) as $\hat{B}_c=\hat{B}-(\hat{B}_b-\hat{B})$, where $\hat{B}$ is computed from Equation 1, $\hat{B}_b$ is the estimate from the bootstrap simulation, and the mean square error ($MSE=variance+bias^2$) of the biomass estimates (Eq. 2).

We also computed a crude estimate of the recruit biomass (age-zero year or incoming year class) as ancillary information for comparative purposes for spring in 2004 and 2005, based on the biomass of fish ≤120 mm SL because 120 mm was the break point for the length-frequency distribution in March surveys from this study (Fig. 6) and it was reported that age-0 sardine in the PNW were ≤110 mm (measured by fork length) (Emmett et al., 2005). Recruit biomass (B_R) was estimated by using Equations 1 and 2, where $\bar{X}_i$= the mean catch (kg/m^2) of fish ≤120 mm SL in the ith stratum ($\bar{X}_{R,i}$). The catch of recruits for each trawl would be obtained as $X_{R,ij}=X_{ij}*U_{ij,\text{ length}\le 120\text{mm}}$, where X_{ij} = the total catch from the jth trawl, and $U_{length\le 120\ mm}$ =the weight of fish ≤120 mm SL divided by the total fish weight based on our random samples with a maximum of 50 fish from each tow.

Spawning habitat

The spawning habitat was defined as the area of relatively high egg densities during early summer, because June–July was the peak spawning time for Pacific sardine off the PNW as determined from egg and larval data collected in the mid-1990s (Bentley et al., 1996). Because the number of positive CalVET tows was low (four of 54 tows during July 2003 and 3 of 48 tows during July 2004), we chose to use data from CUFES sampling. The spawning habitat area was defined as the area where the majority of egg densities exceeded a threshold of 0.5 eggs/min because the egg densities were generally low. Off California,

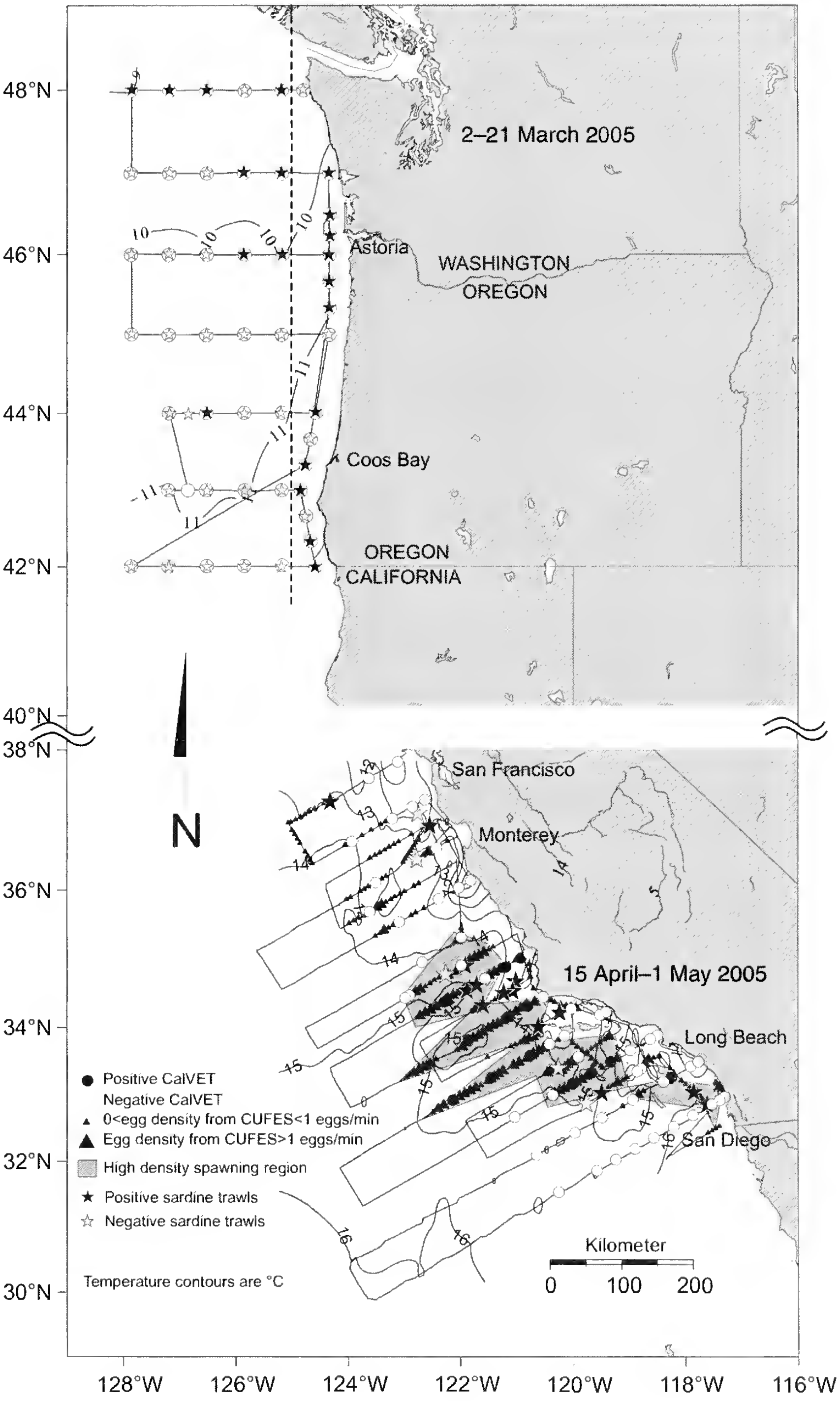

Figure 5

Locations of trawl (stars) and California vertical egg tows (CalVET: circles) for the 2005 March ichthyoplankton-trawl survey off the Pacific Northwest (top) and trawls, CalVET tows (circles), and continuous underway egg samples (CUFES: triangles) for the April–May 2005 California Cooperative Oceanic Fisheries Investigations (CalCOFI) daily egg production survey (bottom). Solid symbols indicate that Pacific sardine (*Sardinops sagax*) were captured in the sample at that site. Contours are sea surface temperatures (°C). The dashed vertical line is the 125°W longitude divider of the two sampling strata. The shaded area is the spawning habitat.

Table 1

Estimates of biomass of Pacific sardine (*Sardinops sagax*), biomass-related parameters for each survey (stratum 1, stratum 2 [with latitude 125°W as the dividing line between them], and the entire survey area), and confidence intervals for biomass and recruits: incoming year class (fish ≤120 mm standard length) in tons (t). Either the coefficient of variation (CV) or number of positive (pos) trawls is in parentheses.

	Stratum 1	Stratum 2	Entire survey area
July 2003			
Mean density (kg/m^3)	$2.41e^{-004}$	$2.2e^{-006}$	$4.85e^{-005}$
Biomass (t) (CV)	192,801(0.57)	7207(0.85)	200,008(0.56)
No of trawls[1] (pos)	38(34)	10(2)	48(36)
No of trawls used for biomass (positive)	17(14)	5(2)	22(16)
Survey area (km^2) (% of entire survey area)	40,043(19)	166,333(81)	206,377(100)
Bootstrap results			
Biomass (t) (CV)	193,946(0.53)	7406(0.82)	201,360(0.51)
Mean square error (MSE)$^{1/2}$	102,174	6094	102,378
Bias-corrected	191,656	7009	198,656
Confidence interval (t)			44,286–421,321
March 2004			
Mean density(kg/m^3)	$2.6e^{-005}$	$4.6e^{-008}$	$5.2e^{-006}$
Biomass (t) (CV)	21,243(0.83)	155(0.7)	21,398(0.82)
Recruits (t)(CV)	21,030(0.83)	69(1.0)	21,099(0.83)
No of trawls (pos)	25(7)	34(2)	59(9)
Survey area (km^2) (%)	40,043(19)	166,334(81)	206,377(100)
Bootstrap results			
Biomass (t) (CV)	22,494(0.81)	155(0.69)	22,650(0.8)
MSE$^{1/2}$	18,260	106	18260
Bias-corrected	19,992	155	20,147
Confidence interval (t)			0–63,017
Recruits (t)(CV)	21,629(0.81)	69(1.02)	21,698(0.81)
MSE$^{1/2}$	17,576	70	17,578
Bias-corrected	20,432	69	20,501
Confidence interval (t)			4749–45,808
July 2004			
Mean density (kg/m^3)	$9.0e^{-005}$	$2.3e^{-006}$	$2.1e^{-005}$
Biomass (t) (CV)	72,206(0.405)	6989(0.992)	79,194(0.379)
No of trawls[1] (pos)	20(16)	38(11)	58(27)
No of trawls used for biomass (pos)	17(15)	30(14)	47(19)
Survey area (km^2) (%)	40,043(21)	150,932(79)	190,975(100)
Bootstrap results			
Biomass(t) (CV)	73,186(0.41)	7299(0.95)	80,485(0.38)
MSE$^{1/2}$	29,723	6928	30,605
Bias-corrected	71,226	6678	77,903
Confidence interval (t)			30,474–146,176
March 2005			
Mean density (kg/m^3)	$3.7e^{-005}$	$2.3e^{-007}$	$7.9e^{-006}$
Biomass (t)(CV)	29,488(0.69)	700(0.57)	30,188(0.68)
Recruits (t) (CV)	55(1.0)	0(0)	54.80(1.0)
No of trawls (pos)	15(11)	34(9)	49(20)
Survey area (km^2) (%)	40,043(21)	150,932(79)	190,976(100)
Bootstrap results			
Biomass (t)(CV)	29,573(0.73)	705(0.57)	30,278(0.72)
MSE$^{1/2}$	21,713	402	21,714
Bias-corrected	29,403	695	30,098
Confidence interval (t)			1800–86,035
Recruits (t) (CV)	56.6(0.98)	0(0)	57(0.98)
MSE$^{1/2}$	56	0	56
Bias-corrected	53	0	53
Confidence interval (t)			70–1640

[1] During the July 2003 cruise, data from 22 out of 48 trawls were used for biomass computation. The total 48 trawls included 38 (34 with sardine) in stratum 1 and 10 (2 with sardine) in stratum 2. During the July 2004 cruise, only data from the first 47 trawls out of 58 trawls were used. The total 58 trawls included 20 trawls (16 with sardine) in stratum 1 and 38 trawls (11 with sardine) in stratum 2.

Table 2

Gross anatomical classification of female and male Pacific sardine (*Sardinops sagax*) gonads.

Gonad code	
Female: Ovary description	
1	*Clearly immature*: Oocytes are not visible. Ovary is very small, translucent or clear, and thin, but with rounded edges (torpedo shaped).
2	*Intermediate*: Individual oocytes are not visible to the unaided eye (no visible yolk or hydrate oocytes in the ovaries), but ovary is not clearly immature. Includes possible maturing and regressed ovaries.
3	*Active*: Yolked oocytes in ovaries visible to the unaided eye in any size or amount, including the smaller opaque oocytes (around 0.4–0.5 mm) to the large yellowish oocytes (about 0.6–0.8mm).
4	*Hydrated*: Hydrated oocytes are present, yolked oocytes may also be seen. Hydrated oocytes (large and transparent), from few to many, or even if loose or “oozing” or “running” from ovary, qualify for this class
Male: Testis description	
1	*Clearly immature*: Testis is very small, knife shaped, translucent or clear, and thin with a flat ventral edge.
2	*Intermediate*: No milt is evident and testis is not clearly immature (includes maturing or regressed testes).
3	*Active*: Milt is present either oozing from the gonopore, in the duct, or in the testis (observed when the testis was cut).

the threshold was one egg/min. We obtained the SST for CUFES samples with $\geq$0.5 eggs/min as a proxy for the oceanographic conditions. No biological variables such as zooplankton volume (Lynn, 2003) were collected during these surveys.

Daily egg production

The daily egg production (P_0) is defined as the newly spawned eggs produced per 0.05 m^2 per day, where 0.05 m^2 was the surface area covered by the CalVET net tow The daily rate of egg production and the daily specific fecundity rate from adult parameters (Lasker, 1985) are needed to compute spawning biomass. In California waters, sardine egg data from CalVET tows and yolksac larval data from both CalVET tows and bongo nets, and sardine ages were used to model the embryonic mortality curve, a negative exponential curve (Lo et al., 1996, 2005):

$$P_t = P_0 \, e^{(-zt)}, \tag{3}$$

where P_t = the daily production rate at age t (days);
z = the daily instantaneous embryonic mortality rate; and
P_0 = the intercept, is the daily egg production at age zero.

Because few eggs were caught during CalVET net tows in July surveys and no eggs were caught in March surveys (Fig. 2–5, Table 3), no attempt was made to estimate egg production for the March surveys. For July surveys, it was impossible to model the egg mortality curve because the mortality curve requires sufficient data on egg abundance for each egg stage and age. Instead, we used an alternative algorithm to estimate P_0, an integral method ($P_{0,I}$) based on the standing stock of eggs from CalVET tows.

The estimate of P_0 ($P_{0,I}$) was based on the relationship between the mean catch of eggs from CalVET tows ($\bar{Y}$) and egg production (P_0) through the integral of P_t over the period from spawning to hatching (t_h). The mean catch of eggs from CalVET tows was a weighted average with the area in each stratum as weight. This method requires prior knowledge of the egg mortality rate and the temperature-dependent hatching time:

$$\bar{Y} = \int_0^{t_h} P_t \, dt = \int_0^{t_h} P_0 e^{-zt} dt. \tag{4}$$

Integrating the above equation yields the estimate of P_0 as a function of the mean egg density, $\bar{Y}$, incubation time, t_h , and the daily instantaneous mortality rate, z:

$$P_{0,I} = \frac{z\bar{Y}}{1 - e^{(-zt_h)}} \tag{5}$$

with variance calculated by using the delta method:

$$\begin{aligned} \operatorname{var}(P_{0,I}) &= \left(\frac{\partial P_{0,I}}{\partial z}\right)^2 \operatorname{var}(z) + \left(\frac{\partial P_{0,I}}{\partial \bar{Y}}\right)^2 \operatorname{var}(\bar{Y}), \\ &= \left(\frac{\bar{Y}[1 - \exp(-zt_h)(1 + zt_h)]}{[1 - \exp(-zt_h)]^2}\right)^2 \operatorname{var}(z) \\ &\quad + \left(\frac{z}{1 - \exp(-zt_h)}\right)^2 \operatorname{var}(\bar{Y}). \end{aligned} \tag{6}$$

The z value was the estimate from the daily egg production method (DEPM) surveys off California in 2003 (0.48 [CV=0.08]) and 2004 (0.25 [CV=0.04]) (Lo et al., 2005) because of the lack of sufficient data to estimate z off the PNW. Age at hatching (in days) was 2.5 days computed from the temperature-dependent sardine egg development model for stage XII given in Lo et al. (1996): $t_h=30.65^* \exp(-0.145^*\text{temp}-0.037^*12)^*12^{1.41}/24$, where temp is the average temperature from positive CUFES collections during the July surveys, and equals 16.4°C and 16.3°C for 2003 and 2004, respectively. This integral estimate is biased upward on the basis of a comparison of $P_{0,I}$ and the P_0 from the nonlinear regression from four California daily egg production surveys and a simple theoretical population. Both cases indicated that the relative bias (rb=$(P_{0,I} - P_0)/ P_{0,I}$) was close to 20% of $P_{0,I}$. Thus the bias-corrected egg production ($P_{0,c}$) would be $P_{0,c}=P_{0,I}\,(1-\text{rb})= P_{0,I}(0.8)$.

The mean density of eggs ($\bar{Y}_i$) (eggs/0.05 m^2) was estimated for each of two strata (i=1,2), with 125°W latitude as the dividing line. The overall mean density ($\bar{Y}$) for the whole survey area was a weighted average with the area in each stratum as the weight and was used to estimate the daily egg production. No estimate of egg production for each stratum was obtained because of the small sample sizes.

To understand the relative contribution of egg production from the PNW area, we computed a ratio of the total egg production in the PNW to the total egg production in the whole area (PNW and California) as $P_{0,1}\,A_1/\sum P_{0,j}\,A_j$, where $P_{0,j}$ is the daily egg production during the peak spawning time in the survey area A_j; j=1 refers to the PNW area in July and j=2 refers to California in April.

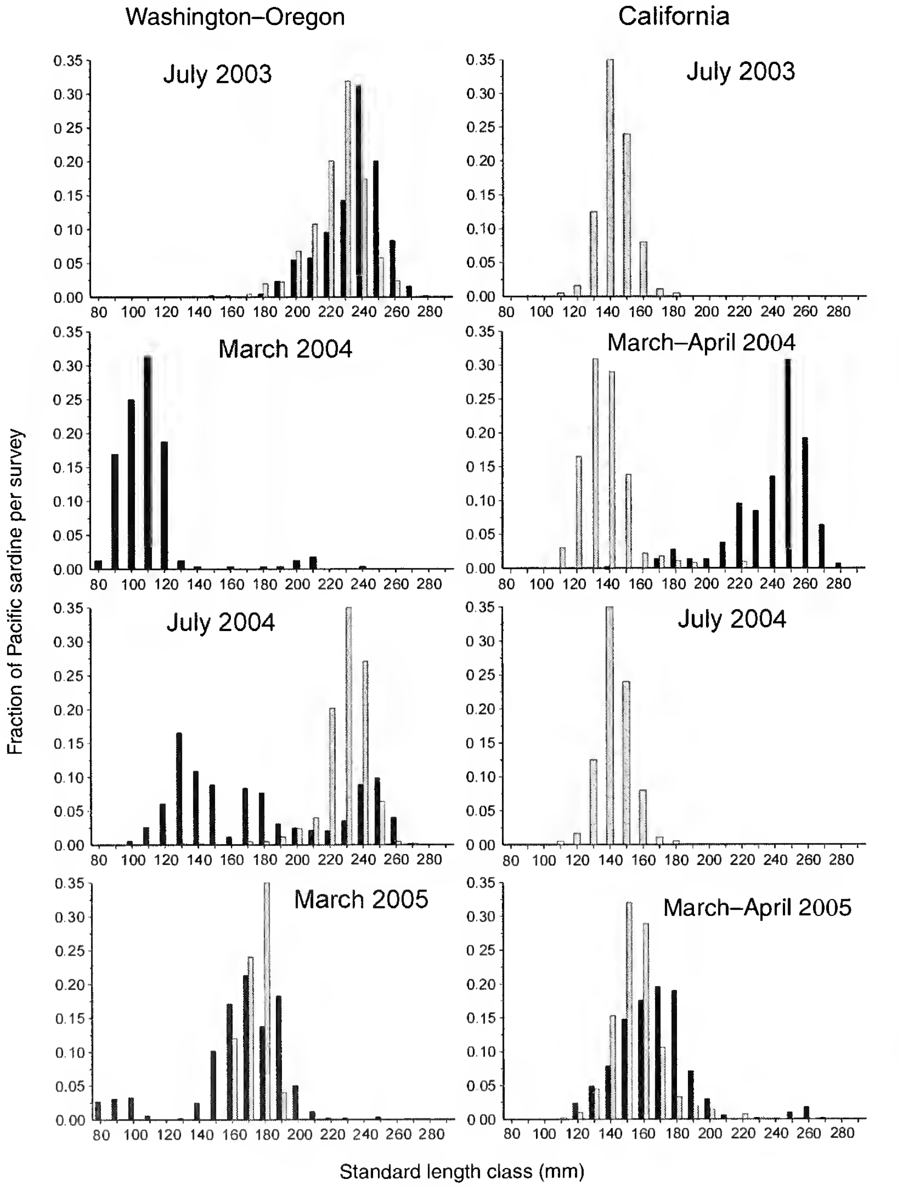

Figure 6

Length frequency distribution of Pacific sardine (*Sardinops sagax*) off Washington and Oregon, and California during 2003, 2004, and 2005 from fishery independent trawl surveys (black bars) and port sampling of commercial purse seine catches (gray bars). Catch data were provided by California Dept. of Fish and Game, Oregon Dept. of Fish and Wildlife, and Washington Dept. of Fish and Wildlife.

Adult reproductive state and parameters

For all four surveys, we used histological analysis of all ovarian tissues, along with trawl and female data, to provide accurate assessment of adult parameters and reproductive state such as maturity, spawning period, recent spawning activity, postspawning condition, or identification of advanced oocyte development for a selection of females for batch fecundity estimation. In the laboratory, each preserved ovary was blotted and weighed to the nearest mg. A piece of each ovary was removed, a histological slide was prepared, and the tissue sections were stained with hematoxylin and eosin. We analyzed oocyte development, atresia, and postovulatory follicle age to assign

Table 3

Estimated Pacific sardine (*Sardinops sagax*) egg densities, egg production ($P_{0,c}$, Eq. 5) with coefficient of variation (CV) in parentheses, and number of collections with positive collections in parentheses from California Cooperative Oceanic Fisheries Investigation vertical egg tow net (CalVET) and continuous underway fish egg sampler (CUFES) samples in two strata with dividing latitude of 125°W and the entire survey area for the July 2003 and July 2004 surveys. Dashes indicate where statistics were not computed because of small or zero catches.

	Stratum 1	Stratum 2	Entire survey area
July 2003			
CalVET			
Egg density (eggs/0.05 m^2)(CV)	0.388(0.51)	0	0.073(0.51)
$P_{0,c}$ (Egg production /0.05 m^2/day)(CV)	—	—	0.04(0.51)
No. of CalVET tows (positive)	18(4)	36(0)	54(4)
CUFES			
Eggs/min (CV)	0.148(0.61)	0.05(0.74)	0.069(0.49)
No of CUFES samples (positive)	316(102)	166(15)	482(117)
Survey area (km^2)(%)	40,043(19)	166,334(81)	206,377(100)
July 2004			
CalVET			
Egg density (eggs/0.05 m^2)(CV)	0.0(—)	0.088(0.56)	0.070(0.56)
$P_{0,c}$ (Egg production /0.05 m^2/day)(CV)	—	—	0.037(0.58)
No. of CalVET tows (positive)	14(0)	34(3)	48(3)
CUFES			
Eggs/min (CV)	0.11(0.42)	0.097(0.67)	0.1(0.53)
No of CUFES samples (positive)	197(65)	450(64)	647(129)
Survey area (km^2)(%)	40,043(21)	150,932(79)	190,975(100)

Table 4

Percentage and average size in each maturity class of Pacific sardine (*Sardinops sagax*) females in the random samples from trawls conducted during four research surveys in 2003–05 off Oregon and Washington. Maturity was based on histological analysis of ovaries.

Survey dates (*n* females)	Maturity class	Percentage of females	Mean standard length (mm)	Mean whole body weight (g)
6–25 July 2003	Immature	0.7	204	124
(690)	Mature	98.3	238	194
29 Feburary–19 March 2004	Immature	97.2	108	14
(108)	Mature	2.8	207	105
6–25 July 2004	Immature	62.2	147	43
(410)	Mature	37.8	240	200
2–21March 2005	Immature	89.2	161	51
(241)	Mature	10.8	195	87

female maturity and reproductive state (Macewicz et al., 1996; Lo et al., 2005).

Sufficient numbers of immature and mature females in the random 50-fish subsample of a positive trawl for estimation of the length at which 50% were mature were collected during July 2004 and March 2005 (Table≈4). Females were grouped into 10-mm length classes and the length at which 50% were mature was estimated by logistic regression: $y=1/(1+e^{-(a+bL)})$, where y = the proportion of mature female sardine and L = the standard length in mm. The length-specific maturation relationships were compared to those off California in April 1994, 2004, and 2005 (Macewicz et al., 1996; Lo et al., 2005).

Because the spawning season occurs in early summer, we used the two sets of July survey data to estimate the following adult reproductive parameters, which were used in the spawning biomass computation based on the daily egg production method (Lasker,1985; Parker, 1985; Lo et al., 2005): the daily spawning fraction (S)

or the fraction of mature females spawning per day; the average batch fecundity (number of eggs per spawning per mature female: F); the fraction of mature fish that were female by weight (sex ratio: R); and the average weight of mature females (g) (W_f). The reproductive parameters were estimated from the data on the first 25 mature females per trawl or all mature females if there were <25 by following the methods in Macewicz et al. (1996). Females with ovaries histologically identified as containing hydrated oocytes (hydrated ovary) have temporarily inflated ovary weights. For each July survey, the relation between wet weight (y) and ovary-free wet weight (x) from mature females lacking hydrated oocytes was determined as $y=-9.0998 + 1.0758x$ in 2003 and $y=-6.316 + 1.05608x$ in 2004. Thus, the observed female weight was adjusted downward for females with hydrated ovaries when calculating average mature female weight (W_f) for each collection by year. During March of 2004 and 2005, adjustments were not necessary and fecundity was not estimated from mature females caught because none of them had ovaries with oocytes in the migratory-nucleus or hydrated stages. Mean batch fecundity was estimated by the gravimetric method for 54 females from 21 trawls from the July surveys. The relationship of batch fecundity to female weight (without ovary) was then determined.

Reproductive adult parameters were summarized for each trawl. Population values were estimated by methods in Picquelle and Stauffer (1985), where estimation of each adult parameter (S, F, W, R) was based on a ratio estimator (Picquelle and Stauffer, 1985; Lo et al., 1996) and used to calculate spawning biomass and its covariance for the July 2003 and July 2004 surveys.

Spawning biomass

The DEPM is a well-accepted method used for estimating spawning biomass for fish with indeterminate fecundity, i.e. multiple spawners (Hunter and Lo, 1993; Stratoudakis et al., 2006) and was used to estimate the spawning biomass of Pacific sardine in this area in 1994 (Bentley et al., 1996). The spawning biomass was computed with the following equation:

$$B_s = \frac{P_0 A C}{RSF / W_f}, \tag{7}$$

where P_0 = the daily egg production/0.05 m^2 at hatching;
A = the survey area in units of 0.05 m^2;
C = the conversion factor from grams (g) to metric tons (t);
R = the fraction of mature fish that is female, by weight (sex ratio);
S = the daily spawning fraction: fraction of mature females spawning per day;
F = the average batch fecundity (number of eggs per spawn per mature female); and
W_f = the average weight of mature females (g).

The denominator (RSF/W_f) is referred to as the daily specific fecundity (number of eggs/population weight [g]/day).

The variance of the spawning biomass estimate ($\hat{B}_s$) was computed from the Taylor expansion in terms of the coefficient of variation (CV) for each parameter estimate and covariance for adult parameter estimates (Parker, 1985; Picquelle and Stauffer, 1985; Lo et al., 1996; 2005):

$$VAR\left(\hat{B}_s\right) = \hat{B}_s^{\,2} \begin{bmatrix} CV\left(\hat{P}_0\right)^2 + CV\left(\hat{W}_f\right)^2 + CV\left(\hat{S}\right)^2 + \\ CV\left(\hat{R}\right)^2 + CV\left(\hat{F}\right)^2 + 2COVS \end{bmatrix}. \tag{8}$$

The last term, involving the covariance term, on the right-hand side is

$$COVS = \sum_i \sum_{i<j} sign \frac{COV\left(x_i, x_j\right)}{x_i x_j}, \tag{9}$$

where x_i=the ith adult parameter estimate, e.g., $x_i=F$ and $x_j=W_f$. The sign of any two terms is positive if they are both in the numerator of B_S or denominator of B_S (Eq. 7); otherwise, the sign is negative. The covariance term is

$$\operatorname{cov}(x_i, x_j) = \frac{[n/(n-1)]\sum_k m_k (x_{i,k} - x_i) g_k (x_{j,k} - x_j)}{\left(\sum_k m_k\right)\left(\sum_k g_k\right)}, \tag{10}$$

where k = k^{th} tow, and $k=1, \ldots, n$;
m_k and g_k = sample sizes; and
$x_{i,k}$ and $x_{j,k}$ = sample means from the k^{th} tow for x_i and x_j, respectively.

Results

Seasonal biomass

The relative abundance of Pacific sardine was higher in summer than in the following spring off the PNW. The bias-corrected seasonal biomass estimates were 198,600 t (CV=0.51) for July 2003, 20,100 t (CV=0.80) for March 2004, 77,900 t (CV=0.38) for July 2004, and 30,100 t (CV=0.72) for March 2005 over an area close to 200,000 km^2 (Table 1). The inshore stratum 1 made up 20% of the survey area. Yet, for all years stratum 1 had over 80% of the biomass. The recruit biomasses (fish ≤120 mm SL) in spring of 2004 and 2005 were quite different: 20,500 t (CV=0.81) for the 2003 year class and 53 t (CV=0.72) for the 2004 year class, respectively. The 2004 point estimate of the recruit biomass, 20,500 t, was greater than that of the total biomass of 20,100 t but this was primarily due to the bias correction based on the bootstrap simulation and the difference was not statistically significant.

The relatively large 2003 year class constituted a major proportion of the total biomass in March 2004, whereas the 2004 year class constituted a very small proportion of the fish in 2005 (Fig. 6). Therefore, the relative abundance of Pacific sardine in the spring of 2004 and 2005 was primarily supported by the strong year class of 2003.

Spawning habitat

The spawning habitat was located east of 125.5°W longitude in July 2003 and 2004 (Figs. 2 and 4), and between 43° and 44.5°N latitude in July 2003, and between 42° and 44.5°N latitude in July 2004. The location of the spawning center, computed as the weighted latitude and longitude with the eggs/min ($\geq$0.5) as the weight, was 124.7°W and 43.7°N in 2003 and 125.13°W and 42.9°N for 2004. Therefore, the spawning habitat shifted southwestward from 2003 to 2004. Because the eggs from the CUFES samples were distributed more to the west, the size of the spawning habitat was 10,716 km^2 for 2003 and 14,260 km^2 for 2004. The spawning habitat, determined from CUFES data, crossed the dividing line of 125°W between two strata based on trawl allocation. For both July cruises, the range of SST in the spawning habitat was 13.4–18.5°C with a mean close to 16°C (15.7°C and 16.0°C for 2003 and 2004). Note that the overall mean SST for July 2003 was 16.2°C (range 9.4–25.3°C) and the mean temperature was 16.8°C (range 9.7–19.9°C) in July 2004. The number of positive CUFES samples was 117 out of 482 in July 2003 and 129 out of 647 in July 2004. Therefore, the proportion of positive samples (24% in 2003, 19% in 2004) was similar during these two years.

Daily egg production

The mean density of eggs was 0.388 eggs/0.05 m^2 (CV=0.51) in stratum 1 and no eggs were caught by CalVET net tows in stratum 2 during the July 2003 survey. The opposite was true for the July 2004 survey: no eggs were caught in stratum 1 and the mean density in stratum 2 was 0.088 eggs/0.05 m^2 (CV=0.56) (Table 3). The overall mean densities were 0.073 eggs/0.05 m^2 (0.51) and 0.07eggs/0.05 m^2 (0.49) for 2003 and 2004, respectively. The bias-corrected estimates of the daily egg production from the integral method ($P_{0,c}$) (Eqs. 5 and 6) in July were 0.04 eggs produced/0.05 m^2/day(CV=0.51) for 2003 and 0.037 eggs produced/0.05 m^2 /day (CV=0.58) for 2004. The mean egg capture rates from CUFES samples for 2003 and 2004 were 0.069 eggs/min (CV=0.49) and 0.1 eggs/min (CV=0.53) (Table 3).

The ratio of the total egg production in the PNW to the total egg production off the U.S. west coast (PNW and California) was 1.46% and 2.2% for 2003 and 2004 and therefore Pacific sardine off the PNW contributed approximately to 1.8% of the total egg production (Table 5).

Adult sardine reproductive parameters and spawning biomass

During the four surveys, 92 of the 214 trawls (Figs. 2–5, Table 1) captured adults or subadults. In the random subsamples from these trawls, 2862 sardine were measured (Fig. 6); standard length ranged from 99–289 mm for females, 106–281 mm for males, and 75–146 mm for individuals of indeterminate sex (where it was difficult to accurately determine sex without microscopic examination). Nearly all females were mature in July 2003 and nearly all were immature in March 2004 (Table 4). Using logistic regression we computed the standard length at which 50% were mature as 195.1 mm and 199.8 mm for July 2004 and March 2005, respectively (Fig. 7).

Mean batch fecundity was estimated for 35 females caught in July 2003 and 19 from July 2004 (Fig. 8). Analysis of covariance showed no differences in the relationship between female weight (without ovary, W_{of}) and batch fecundity (F_b) among years (P=0.531). Combining the data from July 2003 and 2004, we found that the relationship between female weight and batch fecundity, as determined by simple linear regression, was $F_b=-16755 + 372.1W_{of}$ with the $r^2=0.47$. Because the intercept did not differ from zero (P=0.165), we chose the regression without the intercept, which yielded the relationship $F_b=295.83W_{of}$, where W_{of} ranged from 111–322 g (Fig. 8). The latter equation was used to calculate batch fecundity for each mature Pacific sardine female in the July trawl samples.

The population sex ratio (R) for mature fish was 0.534 female (CV=0.04) in July 2003 and 0.568 female (CV=0.05) in July 2004 (Table 5). The 657 mature female Pacific sardine analyzed from July 2003 and 196 from July 2004 were considered a random sample of the population in the area trawled. Population-level estimates of the other adult reproductive parameters were as follows: average batch fecundity (F)=55,986 eggs/spawning event (CV=0.04) in July 2003 and 55,883 eggs/spawning (CV=0.06) in July 2004; daily spawning fraction (S)=0.027 (CV=0.31) in 2003 and S=0.010 (CV=0.74) in 2004; and mean mature female fish weight (W_f=194.36 g (CV=0.02) in 2003, and 193.16 g (CV=0.03) in 2004 (Table 5). The daily specific fecundity was calculated as 4.21 and 1.68 eggs/gm/day in 2003 and 2004, respectively (Table 5). The proportion of active females spawning was 0.05 and 0.025 for July 2003 and 2004, respectively, which meant that the average female was spawning roughly once every 20 to 40 days. None of the three mature females caught in March 2004 or the 37 mature females caught in March 2005 had histological evidence of imminent or recent spawning (hydrating oocytes or postovulatory follicles), and thus S=0; hence, spawning biomass was not estimated for either March (Table 5).

The estimated spawning biomass based on biased corrected egg production from the integral method ($P_{0,c}$)

and the adult reproductive parameters for July 2003 and July 2004 (Eq. 7, Table 5) was 39,184 t (CV=0.57) and 84,120 t (CV=0.93), respectively, for an area close to 200,000 km^2 from 42°N to 48°N off Oregon and Washington.

Discussion

Dynamics of biomass

Off the PNW, the seasonal relative abundances of Pacific sardine based on the swept area method are nonstationary (i.e, not static): high in summer and low in spring. Fish residing in the PNW in spring are those over-wintering, and in the summer the majority of fish ≥190 mm SL are likely those migrating from California. The spatial distribution of the Pacific sardine was similar between summer and spring: high in the inshore area and low in the offshore area. except during March 2005 when small numbers of sardine were caught in the northern offshore area (Fig. 5). This distribution is quite different from that off California where the spatial distribution varied among years (Lo et al., 2005). The PNW biomass estimates, high in July and low in March, together with the differential length distributions are consistent with the conceptual migration schedule of Pacific sardine (a migration route that appears to be similar to that of Pacific hake, *Merluccius productus*), namely of movement to the PNW from California before

Table 5

Trawl information, estimated female adult parameters, egg production, and spawning biomass (estimated by the daily egg production method (DEPM)) for Pacific sardine (*Sardinops sagax*) from July and March surveys conducted from 2003 through 2005 off Washington and Oregon (Pacific Northwest) and from April surveys conducted from 2003 through 2005 off California and in 1994 off California and Mexico. Either the coefficient of variation (CV) or number of positive trawls is in parentheses. na=not available.

		Pacific Northwest				California			
		2003 July	2004 March	2004 July	2005 March	1994 April	2003 April	2004 April	2005 April
No. trawls (positive)		48(36)	59(9)	58(27)	49(20)	79(43)	0	25(17)	19(14)
Ave. surface temperature (°C) at sardine locations		15.4	10.4	15.6	10.4	14.36		13.59	14.18
Fraction of females by weight	R	0.534		0.568		0.538		0.618	0.469
Ave. mature female weight									
(g) with ovary	W_f	194.36	105	193.16	102.5	82.53		166.99	65.34
(g) without ovary	W_{of}	189.25	102.7	188.90	100.2	79.33		156.29	63.11
Average batch fecundity[a]	F	55,986		55,883		24,283		55,711	17,662
Relative batch fecundity (oocytes/g)		288		289		294		334	270
No. mature females analyzed		657	3	196	37	583		290	175
No. active mature females		374	1	81	11	327		290	148
Fraction of mature females[b] spawning per day (CV)	S	0.027 (0.31)	0	0.010 (0.74)	0	0.074 (0.23)		0.131 (0.17)	0.124 (0.31)
Fraction of active females[c] spawning per day	S_a	0.050	0	0.025	0	0.131		0.131	0.155
Daily specific fecundity	$\frac{RSF}{W}$	4.21	na	1.68	na	11.7		27.04	15.67
Egg production/0.05 m^2/day (CV) (Eq. 5)	P_0	0.04[d] (0.51)		0.037[d] (0.58)		0.193 (0.21)	1.520 (0.18)	0.960 (0.24)	1.916 (0.42)
Survey area (km^2)	A	206,037		190,975		380,175	365,906	320,620	253,620
Spawning biomass (t) (CV)	B_s	39,184 (0.57)	na	84,120 (0.93)	na	127,102 (0.32)	485,121 (0.36)	281,639 (0.30)	621,657 0.54
Eggs/min from CUFES sample (CV)		0.069 (0.49)		0.1 (0.53)		na	1.57 (0.27)	0.78 (0.11)	0.62 (0.15)

[a] Mature females: 1994 estimate was calculated with F_b=–10858 + 439.53 W_{of} (Macewicz et al., 1996), in 2004 with F_b= 356.46W_{of}(Lo et al., 2005), in 2005 with F_b=–6085 + 376.28 W_{of}, and for Pacific Northwest in 2003 and 2004 with F_b=295.83 W_{of}.

[b] Mature females included females that were active and those that were postbreeding (incapable of further spawning during the season).

[c] Active mature females were capable of spawning and had oocytes with yolk or postovulatory follicles less than 60 hours old.

[d] Calculated by the integral method and corrected for bias ($P_{0,c}$).

summer to feed, and a return to the south before spring to spawn (Clark and Janssen, 1945; Dorn, 1995; Emmett et al., 2005; Smith, 2005).

The U.S. stock biomass of age 1+ Pacific sardine increased from 1981 to a peak of one million tons in 2000 and, according to the stock assessment, began to decline in 2003 (Hill et al., 2007). The high biomass off the PNW in 2003 was most likely due to the accumulation of migrant survivors from 1999 through 2002, when the stock assessment reported that biomasses were high. The PNW sardine biomass, estimated from surface rope-trawl surveys for salmon off the Columbia River, has been decreasing since 2003 (R. Emmett, personal commun.[2]). This decrease is likely due to 1) the decline of migratory fish as a result of the decreasing biomass since 2003 off California, 2) a decline in successful spawning off the PNW, or 3) the continued sardine movement northward into Canadian waters, or a combination of the three events.

The July 2003 survey indicated that the majority of fish were large (≥190 mm SL), whereas the July 2004 survey showed the opposite because most of the small fish were from the strong 2003 year class. The presence of large sardine off Oregon in July 2003 and California in March–April 2004 is consistent with the concept of the migration of large fish from the PNW to California before spawning. However, the large sardine off Oregon in July 2004 did not show up off either California or the PNW during March–April 2005 (Fig.6). This finding may have been due to a lower total biomass and a smaller proportion of large fish off the PNW in July 2004 (Table 1, Fig. 6), or because during the 2005 California survey, few trawls were taken north of 34°N latitude where most migrants had resided according to the 2004 DEPM survey off California, or it could have been due to a combination of both factors (Fig. 5).

Although the summer PNW biomass estimates were different between years, the spring biomass estimates were stable. March surveys clearly revealed the relative magnitude of the migratory and the local PNW stocks during the survey years. The change in biomass off the PNW among years can be due to multiple reasons: a change in the biomass of the resident PNW fish, or a change in the biomass off California, or a change in the migration pattern due to food availability and oceanographic conditions, or both (MacFarlane et al., 2005). To better understand the dynamics of the Pacific sardine off the west coast of North America, spring and summer synoptic surveys from Baja California, Mexico, to British Columbia, Canada, and from tagging studies are necessary.

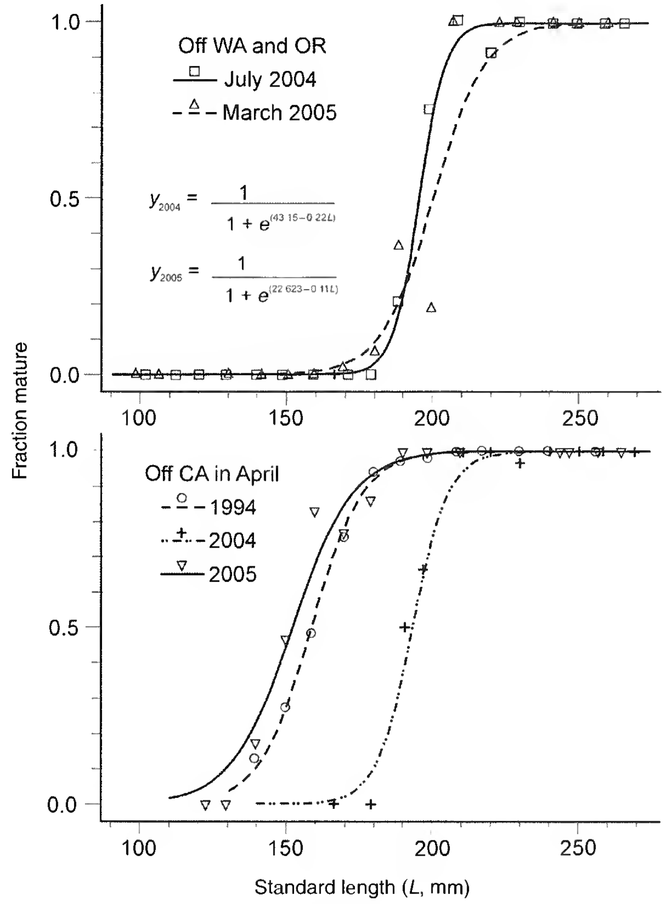

Figure 7

Fraction of Pacific sardine (*Sardinops sagax*) females that were sexually mature (y) as a function of standard length (L) fitted to logistic curves for Oregon and Washington in July 2004 and March 2005, and for California in April of 1994, 2004, and 2005. Symbols represent the actual fraction mature within 10-mm length classes.

Spawning habitat and daily egg production

The spawning habitats off the PNW in the summer of 2003 and 2004 were similar in size between 42–44.5°N and east of 125.4°W. The spawning area occupied 5–7% of the survey area, much smaller than that off California (20–25% of the survey area in 2003–04). The spawning habitat in the mid-2000s (2003 through 2005) seemed to contract southward and shoreward compared to the mid-1990s (1994 through 1998) when it extended to 46°N and close to 126°W (Emmett et al., 2005). The temperature range in the offshore spawning habitat in the 1990s (14–16°C) was similar to that in the 2003–04 inshore area (13–18°C); therefore, the change of oceanographic conditions may have caused the apparent contraction of spawning habitat between the mid-1990s and mid-2000s off the PNW. Because no adult samples were taken in the mid-1990s, we were unable to compare the adult

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[2] Emmett, Robert. 2009. Northwest Fisheries Science Center, Newport, OR.

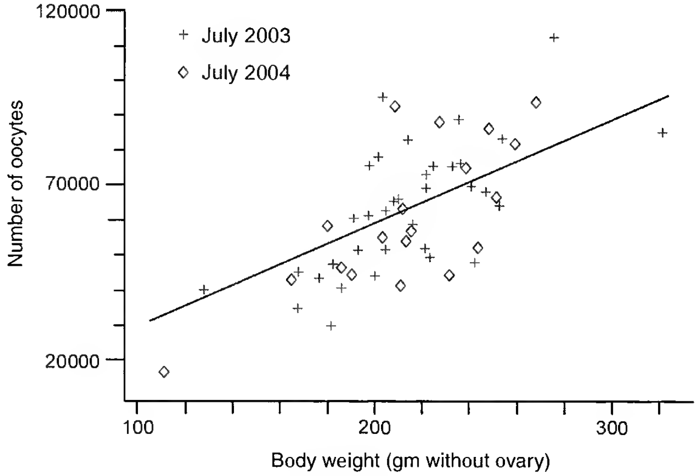

Figure 8

Batch fecundity (F_b), the estimated number of hydrated or migratory-nucleus oocytes, of Pacific sardine (*Sardinops sagax*) as a function of ovary-free fish weight (W_{of}). Pacific sardine females were collected from trawl samples off Oregon and Washington during July 2003 and 2004. Equation for regression line is F_b=295.83W_{of}.

spawning characteristics during these two periods. The spawning habitats of sardine off the PNW in 2003 and 2004 were similar, whereas the spawning habitats off California were quite different: concentrated off central California in 2004 and distributed through the whole survey area in 2005. Note, no eggs were caught during the July California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys off California in either CalVET or bongo net tows.

The daily egg production off the PNW was low in both 2003 and 2004 (0.04 and 0.037eggs produced/0.05 m^2/day, respectively), lower than that in 1994 (0.50 eggs produced/0.05 m^2/day) (Bentley et al., 1996), and lower than those off California (1.52 and 0.96 eggs produced /0.05 m^2/day) in 2003, 2004, and other years. This low egg production in the PNW contributed only 1.8% of the total U.S. west coast egg production in 2003–04. The low PNW egg production estimates could be the result of the July surveys occurring after the spawning peak, possibly in June, as the SST was high (Emmett et al., 2005), or the result of the egg mortality of Pacific sardine off the PNW being different from that off California, or both. Future ichthyoplankton surveys with large sample sizes are needed to obtain direct estimates of the daily egg production and egg mortality off the PNW.

The egg production estimates from July 2003 and 2004 were very similar even though the relative abundances were quite different. With similar egg production in two years, one might expect that the biomass of recruits would be similar. However, the 2003 year class was much stronger than that of 2004. This difference would be most likely due to the more favorable environmental conditions in 2003 than in 2004.

One interesting question to ask is what effect a reduction of the spawning habitat or egg production would have on the PNW Pacific sardine population. The sustainability of the Pacific sardine population off the PNW depends greatly on the Pacific sardine population off California, oceanographic conditions, and food availability (MacFarlane et al., 2005) because most of the spawners (>190 mm SL) off the PNW in the summer are migrants from California. As long as the Pacific sardine population off California is large enough to allow adequate migration to the PNW in the summer to spawn, the population off the PNW will be sustained. Of course, if environmental conditions are unfavorable, the proportion of spawners may be reduced, affecting both the recruits to the local population and the size of the population in the following spring. If the population off California decreases to the level of collapse, the population off the PNW may have been diminished well before the collapse off California. This status of the PNW population was evident from the history of landings in the last Pacific sardine collapse (Fig. 1). During the waning years of sardine population, the PNW commercial landings ended in 1949, 16 years before the California catch ended in 1965. The sardine population began recovering in the late 1970s–early 1980s off California. Incidental landings off California began in 1981, 11 years before an incidental catch of sardine off the PNW in 1992 due to the favorable El Nino conditions, and 17 years before directed landings in 1998.

Application of proper management strategies to preserve the population off California, and thus the migrants, is essential because most of the migrants are mature fish and the leaders of migration imprints: older fish lead younger fish to migrate. This recent entrainment hypothesis (Petitgas et al., 2006) is a step forward from the theory that fish population life cycles are controlled only by physical conditions (Sinclair, 1988). The entrainment hypothesis implies that the older fish are essential to ensure the sustainability of population and fisheries of Pacific sardine off the PNW and thus along the entire west coast of the North American continent.

Adult reproductive parameters and spawning biomass

Pacific sardine spawn off the PNW, contrary to beliefs in the 1930s and 1940s that they spawn only off California. Although sardine eggs, larvae, and adults have been caught in surveys off the PNW since 1994 (Bentley et al., 1996; Emmett et al., 2005), only with the four surveys during 2003–05 were the reproductive parameters for female Pacific sardine off the PNW examined in detail.

The spawning season of Pacific sardine off the PNW apparently occurs primarily in the early summer, although a few fish possibly spawn in spring. If July is the spawning peak off the PNW, then spawning is less intense than during the peak off California in April. The daily spawning fraction of mature females (S=0.027 and 0.01) was much lower than that off California (0.07–0.17). Previous work has indicated that active mature females of *Sardinops* spp. worldwide spawn once every eight days (Macewicz et al., 1996). Recent results off California are similar (once every 6–8 days), where as active mature Pacific sardine females off the PNW spawned much less frequently (only once every 20–40 days). In addition, females in July produced about 288 eggs per gram of female weight (relative batch fecundity) off the PNW—few eggs than similar females off California that spawned 334 eggs per gram of female weight in April 2004 (Table 5). According to the April 2004 DEPM sardine survey off California, the large mature females, in particular those ≥200 mm SL, were spawning very vigorously (S=0.131) and these migratory females may not have recovered sufficiently to spawn at higher rates off the PNW during July 2004, a phenomenon similar to that which occurred with Pacific sardine off Chile, which were less active during a second annual spawning period (Tascheri and Claramunt, 1996). The presence of a high percentage of inactive mature females off the PNW in July (43% in 2003 and 59% in 2004) indicates two other possible explanations for the low level of spawning: July is not the peak spawning time for sardine off the PNW because they may be similar to northern anchovy where ovaries with high levels of atresia (indicating cessation of reproductive activity) are common at the end of the spawning season (Hunter and Macewicz, 1985); or, Pacific sardine in the PNW may behave like chub mackerel (*Scomber japonicus*) whose individuals spawn only for a short period and inactive mature females are common throughout the spawning season (Dickerson et al., 1992). If so, it may be necessary in future surveys to analyze reproductive samples collected over a longer time to better define the peak spawning period, and to determine whether the peak spawning fraction is similar to the rate off California (about 0.13 spawning per day) or whether it remains low (<0.03).

Few mature Pacific sardine females were caught off the PNW during March and it seems that they may have followed warmer water south. The majority of the 40 mature females were inactive (postbreeding or resting) and none had spawned. It was surprising that we caught 12 females of 202–260 mm SL that were active (their ovaries contained some oocytes with yolk) and were potentially capable of spawning in the near future (3–30 days). We examined the locations where females were caught and their associated water temperatures. The average SST of trawls during March was 10.4°C. During March 2004, the three mature females (one active) were caught farthest south (42°N) in 11.1°C water. One inactive mature female was caught near Astoria, OR, in 11.1°C water during March 2005, and the other 36 (11 active) mature females were caught inshore, south of 44.5°N in 11.5°C (10.7–12.5°C) water. Immature female Pacific sardine were generally found north of 44.5°N in cooler water; on average 10.2°C (9.6–10.7°C) in March 2004 and 10.3°C (9.0–12.5°C) in March 2005. Thus, in the winter, the older fish were able to move south following the warmer water, while the younger fish, due to a lack of stored energy for long distance swimming, remained in the cold water. Overwintering immature females seem to tolerate water as cold as 9.0°C. The PNW generally has warmer coastal SSTs in the winter (from downwelling) than in summer. However temperatures in the estuaries can be very cold and die offs of age-0 sardine in the Columbia River and other estuaries have been observed during the winter (E. Dorval, personal commun.[3]).

Female Pacific sardine in the PNW mature at lengths greater than those off California. Fifty percent of the females caught off the PNW matured at around 195 mm and > 90% off California were mature at the size of the smallest mature PNW female (182 mm). A majority of sardine > 200 mm off the PNW migrate during fall–winter (Clark and Janssen, 1945; Nottestad et al., 1999). During the April 2004 DEPM survey, Pacific sardine were collected off central California between 34.8°N and 37.3°N and a majority were the large, migratory size (those ≥200 mm), whereas in 2005, the majority of positive adult samples were collected in the inshore area of Southern California between 32°N and 36°N and most sardines were <200 mm. The length of females at 50% maturity off the PNW was similar to the length estimate (193 mm) in April 2004 off California which indicated that the large Pacific sardines off central California likely were winter migratory fish. This conclusion is consistent with the historical tagging

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[3] Dorval, Emanis. 2008. Librairie La Lumiere, Rue Baussan, # 34, Turgeau, Port-au-Prince, Haiti, W.I.

results, which indicated that the majority of the tags released off the PNW were recovered off central California (Clark and Janssen, 1945).

The point estimates of spawning biomass of Pacific sardine off the PNW differed, but were not statistically different because of a large coefficient of variation: 39,184 t and 84,120 t for July 2003 and 2004, respectively. They were close to 50,000 t in 1994 (Bentley et al., 1996). Theoretically, the spawning biomass should constitute a good proportion of the total biomass, which was not so for July 2003. This could be due to an underestimate of P_0, to an overestimate of the spawning fraction, or both. The overestimate of the spawning fraction could be due to the movement of the postspawners out of the spawning area. A DEPM study is needed to evaluate such effects and model the effects of fish movement on estimates of spawning rate. The effect of the timing of the survey in relation to spawning and movement cycles needs to be studied with new data and modeling.

The difference between the spawning biomass estimates in 2003 and 2004 was primarily due to the difference in the estimated spawning fractions (0.027 in contrast to 0.01), because the estimates of daily egg production (P_0) were similar. The large coefficients of variation of spawning biomass estimates were mainly a result of the uncertainty in estimates of P_0 and the daily spawning fraction (S) in July 2004. For low values of P_0 and S, the number of samples has to be substantially increased to obtain a more precise estimate (Picquelle and Stauffer, 1985). Estimated spawning biomass for off the PNW in July was much smaller than estimates for off California during April in recent years. The smaller fish length at 50% maturity off California means that the more numerous smaller resident Pacific sardine are able to participate in local spawning at the same time as the larger migratory sardine.

Future work

The Pacific sardine spawning habitat and season in the PNW are loosely defined in this study and the magnitude and scope of the coastal migration are not fully explored. To better characterize these, we need to conduct synoptic trawl-ichthyoplankon-acoustic surveys from Baja California, Mexico, to British Columbia, Canada, during spring and early summer at three to five year intervals. To better characterize the spawning habitats in this area, we need to obtain physical and biological oceanographic data (Lynn, 2003; Emmett et al., 2005; Reiss et al., 2008) and demographic data of Pacific sardine over a broader geographic range because the Pacific sardine is a migratory species.

For trawl swept-area–based biomass estimates, the efficiency of the trawl needs to be calibrated. Biomass estimates from acoustic surveys would be another fishery-independent source of relative abundance. Because the coefficients of variation of all estimates are large, the number of trawls needs to be increased or other statistical estimation procedures should be explored, or both, to improve the precision of estimates. To obtain a representative length distribution of the population, fishery-independent surveys covering the whole west coast area are essential, and length data from commercial vessels should be used with caution for both the PNW and California. For spawning biomass, we need to understand the maturation schedules of females and the spawning season off Oregon and Washington. Numerous plankton net tows are needed to obtain direct estimates of the daily egg production and egg mortality rates in early summer. Currently, only the spawning biomass of Pacific sardine off California is estimated from the annual April DEPM survey. Because mature females were caught during two March surveys off the PNW, efforts should be made to obtain trawl data off the PNW in April. Data for mature females collected off the PNW could then be combined with the April data set off California to estimate reproductive parameters and the spawning biomass of Pacific sardine off the whole west coast of the United States. To better understand the relationship between the sardine populations off California and the PNW, we need to examine migration characteristics (i.e, migration range, pattern and schedule) and the effect of fishing pressure on the migratory fish because most of these fish are mature and leaders of migration imprints. We need a long time series of abundance for all regions together, along with oceanographic and biological data, to enhance our understanding of the dynamics of the entire Pacific sardine population to provide information for the development of future strategies to sustain the population.

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Seasonal variability in ichthyoplankton abundance and assemblage composition in the northern Gulf of Mexico off Alabama

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Abstract—Multiyear ichthyoplankton surveys used to monitor larval fish seasonality, abundance, and assemblage structure can provide early indicators of regional ecosystem changes. Numerous ichthyoplankton surveys have been conducted in the northern Gulf of Mexico, but few have had high levels of temporal resolution and sample replication. In this study, ichthyoplankton samples were collected monthly (October 2004–October 2006) at a single station off the coast of Alabama as part of a long-term biological survey. Four seasonal periods were identified from observed and historic water temperatures, including a relatively long (June–October) "summer" period (water temperature >26°C). Fish egg abundance, total larval abundance, and larval taxonomic diversity were significantly related to water temperature (but not salinity), with peaks in the spring, spring–summer, and summer periods, respectively. Larvae collected during the survey represented 58 different families, of which engraulids, sciaenids, carangids, and clupeids were the most prominent. The most abundant taxa collected were unidentified engraulids (50%), sand seatrout *(Cynoscion arenarius,* 7.5%), Atlantic bumper (*Chloroscombrus chrysurus,* 5.4%), Atlantic croaker (*Micropogonias undulatus,* 4.4%), Gulf menhaden (*Brevoortia patronus,* 3.8%), and unidentified gobiids (3.6%). Larval concentrations for dominant taxa were highly variable between years, but the timing of seasonal occurrence for these taxa was relatively consistent. Documented increases in sea surface temperature on the Alabama shelf may have various implications for larval fish dynamics, as indicated by the presence of tropical larval forms (e.g., fistularids, labrids, scarids, and acanthurids) in our ichthyoplankton collections and in recent juvenile surveys of Alabama and northern Gulf of Mexico seagrass habitats.

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Ichthyoplankton surveys provide fisheries-independent information that is inherently "ecosystem-based"; entire larval fish assemblages are collected (i.e., early stages of both exploited and unexploited finfish species) along with zooplankton predators and prey, and often with a suite of environmental observations (e.g., salinity, temperature). At the ecosystem level, information on larval assemblages can be used to detect changes in marine fish community composition and abundances over time (Sherman et al., 1984). Previous studies have indicated that larval assemblages are the result of convergent spawning strategies by multiple species taking advantage of favorable environmental conditions for larval fish survival (Doyle et al., 1993; Sherman et al., 1984). The composition of larval fish assemblages varies spatially and temporally because of the behaviors of the larvae (Gray and Miskiewicz, 2000; Hare and Govoni, 2005) and the spawning adults (Sherman et al., 1984; Hernández-Miranda et al., 2003), as well as oceanographic transport and mixing processes (Auth, 2008; Muhling et al., 2008). Variability in any of these factors, therefore, may result in a different structure of larval fish assemblages. Because larval fish survival is closely tied with primary and secondary productivity in coastal oceans, changes in larval fish assemblage structure (over larger time scales) can be an early indicator of climate-related environmental shifts (Auth, 2008; Brodeur et al., 2008).

Despite the importance of the region to fisheries, seasonal variability in larval fish assemblages in the northern Gulf of Mexico has been examined in relatively few studies. Much of the previous ichthyoplankton research has focused on estuarine assemblages (Raynie and Shaw, 1994; Tolan et al., 1997) or on relatively short-term interactions between assemblages and specific oceanographic features, such as the Mississippi River plume (Sogard et al., 1987; Govoni et al., 1989) or the Loop Current (Richards et al., 1993). Other studies have used ichthyoplankton survey data from the National Marine Fisheries Service's (NMFS's) gulf-wide Southeast Monitoring and Assessment Program (SEAMAP), but these studies are typically focused on a single species (Scott et al., 1993; Lyczkowski-Shultz and Ingram, 2003; Lyczkowski-Shultz and Hanisko, 2007). Ditty et al. (1988) summarized the available ichthyoplankton literature at the time to provide information on larval fish seasonality for the entire northern Gulf of Mexico, and more

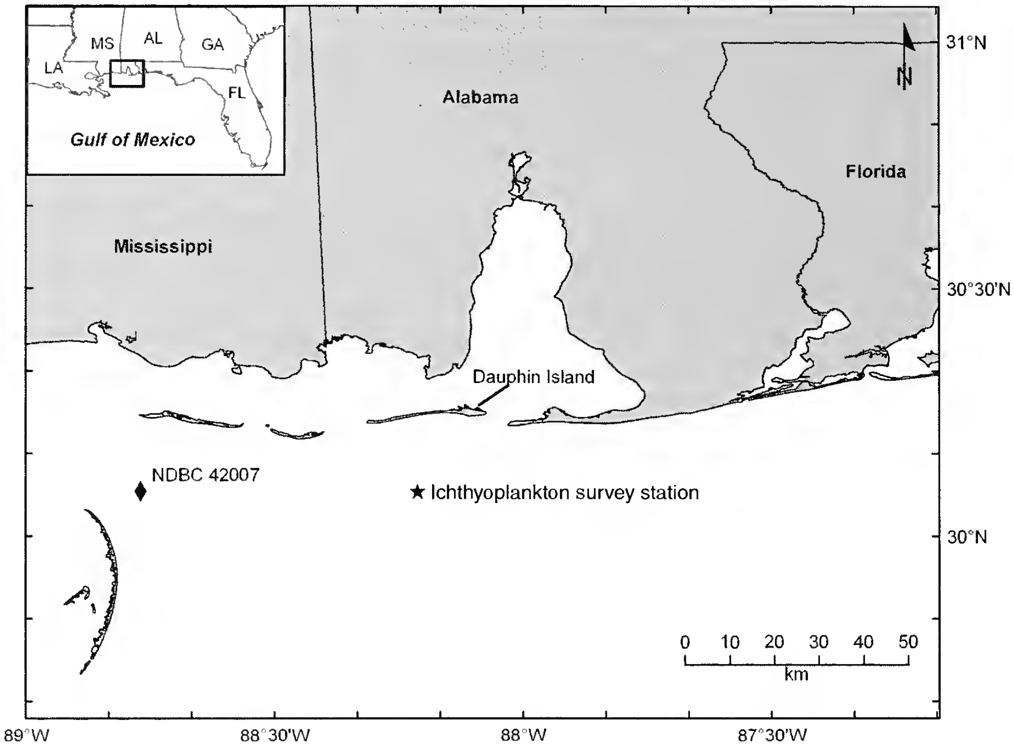

Figure 1

Location of the sampling station used during the October 2004–October 2006 ichthyoplankton monitoring survey (star symbol) and the NOAA National Data Buoy Center oceanographic data buoy (NDBC 42007) used to determine the 10-year (1993–2003) mean monthly water temperature estimates for the region (diamond symbol).

recently, Lyczkowski-Shultz et al.[1] reported on larval fish seasonality and distribution for the northeastern Gulf of Mexico.

Although these latter studies provided information on multiple species, no analyses of larval fish assemblages and environmental variability were presented. Here we report on the seasonality and concentrations of larval fishes in relation to water temperature based on data collected during an intensive two year (October 2004–October 2006) ichthyoplankton survey conducted off the coast of Alabama. The objectives of this study were 1) to examine the seasonal variability in ichthyoplankton diversity and taxon-specific abundances off the coast of Alabama; and 2) to examine variability in the relationship between larval fish assemblages and seasonal changes in water temperature. These objectives would contribute to our overall goal of understanding the oceanographic factors that maintain larval fish assemblages.

Materials and methods

Data collection

The sampling station was located on the inner continental shelf of the northern Gulf of Mexico, approximately 18 km south of Dauphin Island, Alabama, at a water depth of approximately 20 m (Fig. 1). Ichthyoplankton sampling was conducted during monthly day-time surveys (n=26) and quarterly diel surveys (n=8) from October 2004 to October 2006 (Table 1). All samples were collected with a Bedford Institute of Oceanography Net Environmental Sampling System (BIONESS) (Open Seas Instrumentation, Inc., Musquodoboit Harbour, Nova Scotia, Canada), with a 0.25-m^2 mouth opening fitted with seven (during quarterly surveys) or eight (during monthly surveys) plankton nets. During monthly surveys, six depth-discrete samples (18–15 m, 15–12 m, 12–9 m, 9–6 m, 6–3 m, and 3–1 m) and one oblique sample (18–1 m) were collected during eight replicate tows at the study site with 202-μm mesh nets. An additional oblique sample was collected during each tow with a 333-μm mesh net for a nominal total of 64 samples per monthly cruise. All eight replicate tows were collected during daylight hours, generally during a single day. During the quarterly surveys, a set of six depth-discrete samples (same depth bins as monthly survey) and one

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[1] Lyczkowski-Shultz, J., D. S. Hanisko, K. J. Sulak, and G. D. Dennis III. 2004. Characterization of ichthyoplankton within the U.S. Geological Survey's northeastern Gulf of Mexico study area—based on analysis of Southeast Area Monitoring and Assessment Program (SEAMAP) sampling surveys, 1982–1999, 136 p. NEGOM Ichthyoplankton Synopsis Final Report, U.S. Dep. Interior, U.S. Geological Survey, USGS SIR-2004-5059.

Table 1

Station data for ichthyoplankton samples collected during a larval fish monitoring survey at a site located approximately 18 km south of Dauphin Island, Alabama (October 2004–October 2006). Seasonal classification is based on historic (10-year average) and observed monthly mean temperatures for the region (see Fig. 2).

Year	Cruise date	Survey type	Seasonal classification	Number of samples
2004	22 Oct	monthly	Summer	54
2004	16–17 Nov	diel	Fall	41
2004	29 Nov	monthly	Fall	47
2004	08 Dec	monthly	Fall	47
2005	06–07 Jan	monthly	Winter	48
2005	18–21 Jan	diel	Winter	76
2005	16 Feb	monthly	Winter	50
2005	29 Mar	monthly	Spring	23
2005	05 Apr	monthly	Spring	18
2005	19 Apr	monthly	Spring	47
2005	09–13 May	diel	Spring	72
2005	17 May	monthly	Spring	48
2005	09 Jun	monthly	Summer	47
2005	13 Jul	monthly	Summer	48
2005	09 Aug	monthly	Summer	46
2005	14 Sep	monthly	Summer	48
2005	27–29 Sep	diel	Summer	72
2005	11 Oct	monthly	Summer	31
2005	09 Nov	monthly	Fall	32
2005	29 Nov–02 Dec	diel	Winter	71
2005	16 Dec	monthly	Winter	40
2006	12 Jan	monthly	Winter	44
2006	07–10 Feb	diel	Winter	60
2006	17 Feb	monthly	Winter	43
2006	16 Mar	monthly	Spring	39
2006	12–13 Apr	monthly	Spring	38
2006	01–04 May	diel	Spring	70
2006	17 May	monthly	Spring	43
2006	15 Jun	monthly	Summer	42
2006	05 Jul	monthly	Summer	46
2006	10 Aug	monthly	Summer	46
2006	08 Sep	monthly	Summer	46
2006	19–22 Sep	diel	Summer	66
2006	12 Oct	monthly	Summer	47

oblique sample were collected with 202-μm mesh nets at dawn, noon, dusk, and midnight (local time) over the course of three diel periods for a nominal total of 84 samples per quarterly cruise. Contents of nets were rinsed with seawater, sieved, and preserved in 4% formalin for 48 hours before being transferred to 70% ethanol. A conductivity-temperature-depth probe (CTD) (SBE19, Sea-Bird Electronics, Inc., Bellevue, WA) was integrated into the BIONESS system and provided temperature, salinity, and depth profiles for each plankton tow. A flowmeter (General Oceanics, Miami, FL) mounted within the BIONESS frame estimated the volume of water filtered for each sample. Filtered volume estimates for each sample were compared with measurements from a second, externally mounted flowmeter to estimate filtration efficiency. In all, 1634 ichthyoplankton samples were processed and used in subsequent analyses. Although all fish larvae were collected from a single station, Alabama has a relatively short coastline (<85 km), thus the larval fishes collected likely represent the ichthyofauna of the entire Alabama inner shelf region.

Preparation of environmental data

CTD data were processed using the manufacturer's software (SEASOFT, Seabird Electronics, Inc., Bellevue, WA) and averaged into 0.5-m bins. Seasonal patterns in water temperature were examined using depth-integrated monthly mean temperatures recorded during each sampling month. For historic comparisons, the 10-year average for water temperature was calculated for each month with data from a coastal observing buoy (NOAA National Data Buoy Center Station 42007) located approximately 54 km west of our sampling station at a water depth of approximately 15 m (Fig. 1). Although the temperature values from the buoy were measured near the surface (0.6-m depth), these observations serve as good indicators of seasonal shifts in water-column thermal structure, as indicated by our own CTD comparisons of sea surface temperature and depth-integrated temperature (correlation coefficient, r^2=0.98; slope, m=0.90; P<0.0001). Together, these data were used to define ecologically relevant "seasons" (rather than calendar date) for multivariate analyses.

Preparation of ichthyoplankton data

Ichthyoplankton samples were sorted and larval fish were identified to the lowest possible taxonomic level at the Plankton Sorting and Identification Center (Szczecin, Poland) and at the Dauphin Island Sea Laboratory (Dauphin Island, Alabama). Many larval fishes were not identified to the species level, owing to the relatively small sizes of larvae collected in the 202-μm mesh nets and the overall diversity of larval forms present in the western central Atlantic region, which includes the Gulf of Mexico (Marancik et al., 2005). Most identifications were at the family level (52%), followed by species (22%), order (14%), and genus (7%) level identifications. Five percent of the larvae collected were damaged or unidentified.

Unidentified clupeiforms (engraulids and clupeids) were excluded from further analyses because their extreme concentrations and taxonomic ambiguity can often mask abundance and assemblage trends (Tolan et al., 1997; Hernandez et al., 2003). Order-level taxa and unidentified larvae were removed from consideration for similar reasons. Further taxonomic analyses, therefore, were limited to taxa that represented at least 1% of the total catch during any individual sampling event, where the proportion of the total catch for each taxonomic group was determined after removing unidentified larvae, order-level larvae, and all unidentified clupeiforms. Following Marancik et al. (2005), we further modified the data sets to exclude genus-level groupings in instances where many congeners could potentially mask any seasonal trends. The following genus-level groupings were retained because each represented relatively few congeners with likely similar early life histories in the northern Gulf of Mexico: *Auxis* spp. (*A. rochei* and *A. thazard*), *Centropristis* spp. (*C. philadelphica*, *C. ocyurus,* and *C. striata*), *Diplectrum* spp. (*D. bivattatum* and *D. formosum*), *Microdesmus* spp. (*M. lanceolatus* and *M. longipinnis*), and *Paralichthys* spp. (*P. albigutta*, *P. lethostigma,* and *P. squamilentus*). Similarly, all family-level groups were removed except Gerreidae (most likely *Eucinostomus gula* or *E. argentus*) and Labridae (most likely *Xyrichtys novacula*). In all, 30 taxa were considered for analyses (Table 2). Because the objective of this study was to examine the seasonal variability of larval fish occurrence and relative larval fish concentrations and not size-selectivity or vertical distribution, our analyses included ichthyoplankton data collected from all surveys (monthly and quarterly diel), mesh sizes (202 μm and 333 μm), and depth bins. Depth stratification and gear selectivity will be addressed in separate analyses in forthcoming publications.

Analyses

All fish egg and larval fish abundances were standardized by the volume filtered to determine concentration estimates (no./m^3). Taxonomic diversity was calculated for each sample by taking the exponential of Shannon entropy, exp(H), following the method of Jost (2006). Monthly mean observations of total fish eggs, total fish larvae, and taxonomic diversity were compared to mean temperature and salinity data by using least squares regressions. Two approaches were used to examine larval fish seasonality. First, monthly mean concentrations (no./100 m^3) were calculated for the dominant taxa to examine monthly trends in abundance. Second, observed and historic water temperature observations were used to define distinct seasons for the sampling region. Seasonality in fish egg concentrations, total larval fish concentrations, and taxonomic diversity was examined (after log+1 transformation) by using one-way ANOVAs with season as a factor and Tukey's honesty significant difference (HSD) tests. Lastly, larval concentrations for dominant taxa were square-root transformed and analyzed by using Bray Curtis similarity and cluster analysis with the PRIMER statistical package (PRIMER, vers. 6, Plymouth Marine Laboratory, Plymouth, U.K.).

Results

Mean monthly water temperature varied seasonally over the two year period, with a low of 16.5°C (January 2005) and a high of 30.2°C (August 2006) (Fig. 2). The general pattern of our monthly temperature observations was similar (±2°C) to that of recent historical values (Fig. 3). Notable deviations were relatively cooler temperature observations in May during our study (mean differences of 3.2°C and 2.4°C during 2005 and 2006, respectively) and warmer temperatures in October (mean differences of 2.6°C and 3.0°C during 2005 and 2006, respectively) and December (mean difference of 3.0°C in 2004). Even with these disparities, both data sets were in agreement to define seasonal breaks in water temperature. (Fig. 3). Sampling periods with mean water temperature values <18°C were classified as winter, and those with mean water temperatures above 26°C were classified as summer. The transitional periods of spring and fall had mean water temperatures between 18°C and 26°C. In general, the observed seasonal pattern comprised three-month winter (December–February) and spring (March–May) seasons, a relatively long five-month summer period (July–October), and a relatively

Table 2

Seasonal (X) and peak (*) occurrence of the dominant larval fish taxa collected in plankton samples (n=1634) off the coast of Alabama from October 2004 to October 2006. Seasonal classification is based on historic (10-year average) and observed monthly mean temperatures for the region. (see Fig. 2).

		Season			
Family	Taxon	Winter	Spring	Summer	Fall
Elopidae	*Elops saurus*	*		X	X
Ophichthidae	*Myrophis punctatus*	X	X		*
Clupeidae	*Brevoortia patronus*	*	X	X	X
	Etrumeus teres	X	*		X
	Harengula jaguana		X	*	
	Opisthonema oglinum		*	X	
Serranidae	*Centropristis* spp.	X	X	*	
	Diplectrum spp.		X	*	
	Serraniculus pumilio		X	*	
Carangidae	*Chloroscombrus chrysurus*		X	*	
	Decapterus punctatus		X	*	
Lutjanidae	*Lutjanus campechanus*			*	
Gerreidae	Unidentified		X	*	
Sciaenidae	*Cynoscion arenarius*	X	X	*	
	Cynoscion nothus		X	*	X
	Larimus fasciatus	X	X	*	X
	Leiostomus xanthurus	X	X	X	*
	Micropogonias undulatus	X	X	*	X
	Sciaenops ocellatus			X	
Labridae	Unidentified		X	*	
Microdesmidae	*Microdesmus* spp.		X	*	
Scombridae	*Auxis* spp.		X	*	
	Euthynnus alletteratus		X	*	
	Scomberomorus maculatus		X	*	
Stromateidae	*Peprilus alepidotus*		X	*	
	Peprilus burti	X	X	*	X
Paralichthyidae	*Citharichthys spilopterus*	*	X	X	X
	Etropus crossotus		*	X	
	Paralichthys spp.	X	X	*	X
	Syacium papillosum		*	X	

short one-month fall period (November). In one instance, the interannual variability in water temperature at our sampling site allowed for the same month to be designated as a different season during different years (December was classified as "fall" in 2004 and "winter" in 2005) (Table 1).

No seasonal pattern in salinity was observed at the sampling station (Fig. 3). Salinity observations were generally lower and more variable during the first year of the study, with values fluctuating between 30.4 and 34.6 between October 2004 and September 2005. Salinity was generally higher and less variable between October 2005 and October 2006, with values ranging between 33.0 and 34.8.

A total of 504,478 fish eggs and 311,970 fish larvae were collected over the course of the survey. Total fish egg concentrations during the survey ranged from 0.16 to 48.3 eggs/m^3 (Fig. 3). Egg concentrations were significantly higher in the spring than in other seasons (F=271.3, P<0.0001, spring>summer>fall>winter). Total fish larvae concentrations ranged from 0.15 to 35.0 larvae/m^3 (Fig. 3). Larval concentrations were significantly higher during summer and spring seasons (F=206.1, P<0.0001, spring=summer>fall>winter). The diversity of ichthyoplankton assemblages, exp(H), ranged from 1.32 to 9.48 and was also highest during the summer seasons (F=299.3, P<0.0001, summer>spring>fall>winter) (Fig. 3). Species diversity was significantly related to temperature as determined by a least squares regression (F=34.7, P<0.001, r^2=0.60). Although also significantly correlated, the relationships between temperature and fish egg concentrations (F=4.4, P<0.05, r^2=0.16) and total larval concentrations (F=6.9, P<0.05, r^2=0.23) were not as strong. No significant relationships were observed between salinity and fish eggs (F=0.22, P=0.64, r^2=0.01), total fish larvae (F<0.01, P=0.94,

r^2<0.01), and taxonomic diversity (F=0.16, P= 0.69, r^2=0.01).

Excluding order-level larvae and unidentified larvae, unidentified engraulids dominated our collections and represented approximately 50% of the total (overall) catch (Table 3). Engraulid larvae were present year-round and likely comprised several commonly occurring species in the region, including *Anchoa hepsetus, A. nasuta, A. mitchilli*, and *Engraulis eurystole*. No attempt was made to examine these fishes beyond the family level because many were relatively small (<10 mm) and damaged, and engraulid identifications are problematic in our region (Farooqi et al., 2006a). Other taxa that represented over 1% of the overall catch included *Cynoscion arenarius* (7.5%), *Chloroscombrus chrysurus* (5.4%), *Micropogonias undulatus* (4.4%), *Brevoortia patronus* (3.8%), unidentified Gobiidae (3.6%), unidentified Sciaenidae (2.8%), unidentified Ophidiidae (2.5%), *Symphurus* spp. (2.1%), *Menticirrhus* spp. (1.2%), unidentified Clupeidae (1.2%), *Syacium* spp. (1.2%), and *Etropus crossotus* (1.0%).

Larval fish specimens collected during the survey represented 58 different families. Larvae belonging to 22 of these families could not be identified beyond the family level, usually because published descriptions of representative species in our region are either lacking or are insufficient to discern between different species within the family (e.g., Gerreidae, Sparidae, Haemulidae, Echeneidae, Labridae, Scorpaenidae). Several families were well represented with numerous species or genera, including Ophichthidae (11 identified species), Sciaenidae (9 species), Carangidae (7 species), Myctophidae (6 genera), Paralichthyidae (5 genera), and Clupeidae (5 species). Overall, the dominant families collected during our survey (e.g., Engraulidae, Sciaenidae, Carangidae, and Clupeidae) are the same as those from previous surveys in the general vicinity (Table 3). In general, the taxonomic richness observed in our survey falls between that found in surveys of shorter duration and in limited spatial-scale surveys (e.g., Williams,1983; Rakocinski et al., 1996) and from SEAMAP surveys that encompass a larger area and longer (20 years) time scales (ENTRIX, 2006).

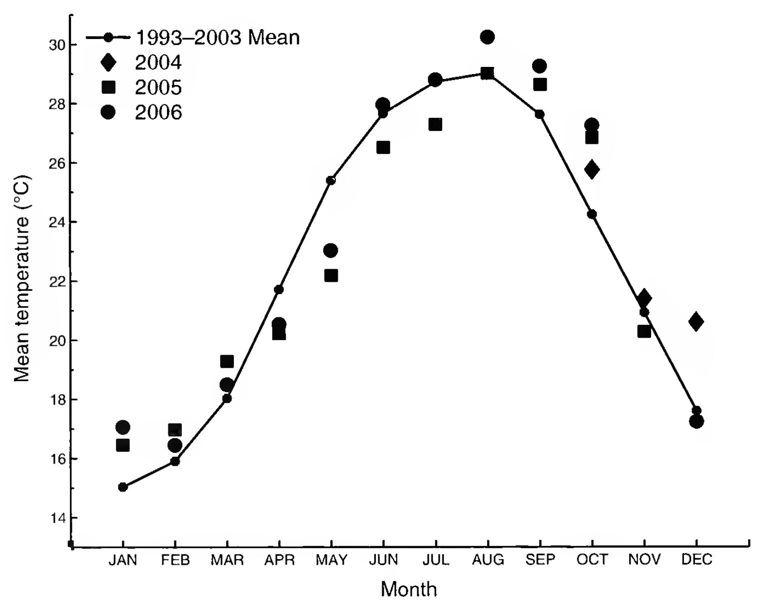


Figure 2

Mean monthly temperature observations (depth-integrated) at the ichthyoplankton sampling station and the 10-year average temperature (1993–2003). Sampling station means are derived from temperature profile observations recorded by the Bedford Institute of Oceanography Net Environmental Sampling System (BIONESS). The 10-year mean was determined from near-surface (0.6 m depth) temperature observations (T_s) recorded by an oceanographic buoy located approximately 54 km west of the sampling station. The plotted depth-integrated temperature estimates (T_i) were calculated through the relation ship $T_i = 0.90*T_s + 2.37$.

Seasonal patterns were observed for most of the dominant taxa collected (Fig. 4). *Lutjanus campechanus* and *Chloroscombrus chrysurus* were collected only during the summer periods (June–October). Similarly, *Sciaenops ocellatus* larvae were collected only during late summer (September–October). In contrast, *Citharichthys spilopterus* was collected in almost every sampling event, indicating year-round spawning or extended pelagic larval durations. Although several species had winter peaks, none were present exclusively during winter months. *Brevoortia patronus* and *Paralichthys* spp., for example, peaked in concentration during November–December, but were also collected in fall–spring. Similar patterns were observed for *Elops saurus* and *Micropogonias undulatus* (late summer–winter) and *Peprilus burti* and *Leiostomus xanthurus* (late summer–spring). *Etrumeus teres* differed in that larvae were collected during winter–spring periods. Most of the dominant taxa, however, were collected primarily during the late spring–late summer months (May–October), such as *Myrophis punctatus, Harengula jaguana, Opisthonema oglinum, Centropristis* spp., *Diplectrum* spp., *Serraniculus pumilio, Decapterus punctatus, Auxis* spp., *Euthynnus alletteratus, Scomberomorus maculatus, Peprilus alepidotus, Syacium* spp., gerreids, and microdesmids. The remaining taxa (*Cynoscion arenarius, C. nothus, Larimus fasciatus*, labrids, and *Etropus crossotus*) were collected during the same period, but inclusive of the early spring months (March–April).

Larval concentrations among the dominant taxa varied widely throughout the survey period (Fig. 4). Several taxa were present in low numbers throughout the survey. For example, mean densities of *E. saurus, O. oglinum, Diplectrum* spp., *S.*

pumilio, L. campechanus, Gerreidae, *S. ocellatus,* Labridae, *Auxis* spp., *E. alletteratus, P. burti, C. spilopterus, Paralichthys* spp., and *Syacium* spp. did not exceed 10 larvae/100 m^3 during any sampling event. Other taxa were characterized by relatively high concentrations, either during a single sampling event (e.g., *E. teres, C. chrysurus, C. arenarius, L. xanthurus, Microdesmus* spp., *S. maculatus, P. alepidotus*) or during a single year (e.g., *H. jaguana*). The remaining taxa (*M. punctatus, B. patronus, Centropristis* spp., *D. punctatus, C. nothus, L. fasciatus, M. undulatus, E. crossotus*) were present during multiple years in relatively similar concentrations.

Results from the cluster analysis were largely in agreement with the observed seasonal patterns previously defined by water temperature (Fig. 5). Taxonomic assemblages from fall and winter periods were clustered separately from spring and summer periods. All summer months (June–October) were clustered together with the exception of August 2005 and October 2004. Larval collections in August 2005 were characterized by atypically high concentrations of a few species, most notably *C. chrysurus* and *C. arenarius,* which were present in concentrations exceeding >500 larvae/100 m^3 (Fig. 4), resulting in relatively low species diversity (Fig. 2) for the summer period. The October 2004 sampling event was included in the summer period, although the mean temperature was marginally below the 26°C criterion for the summer period (Fig. 3) and indicative of a seasonal transitional period. Similarly, the assemblages from the May sampling events were relatively distinct from the earlier spring period sampling events (March and April).

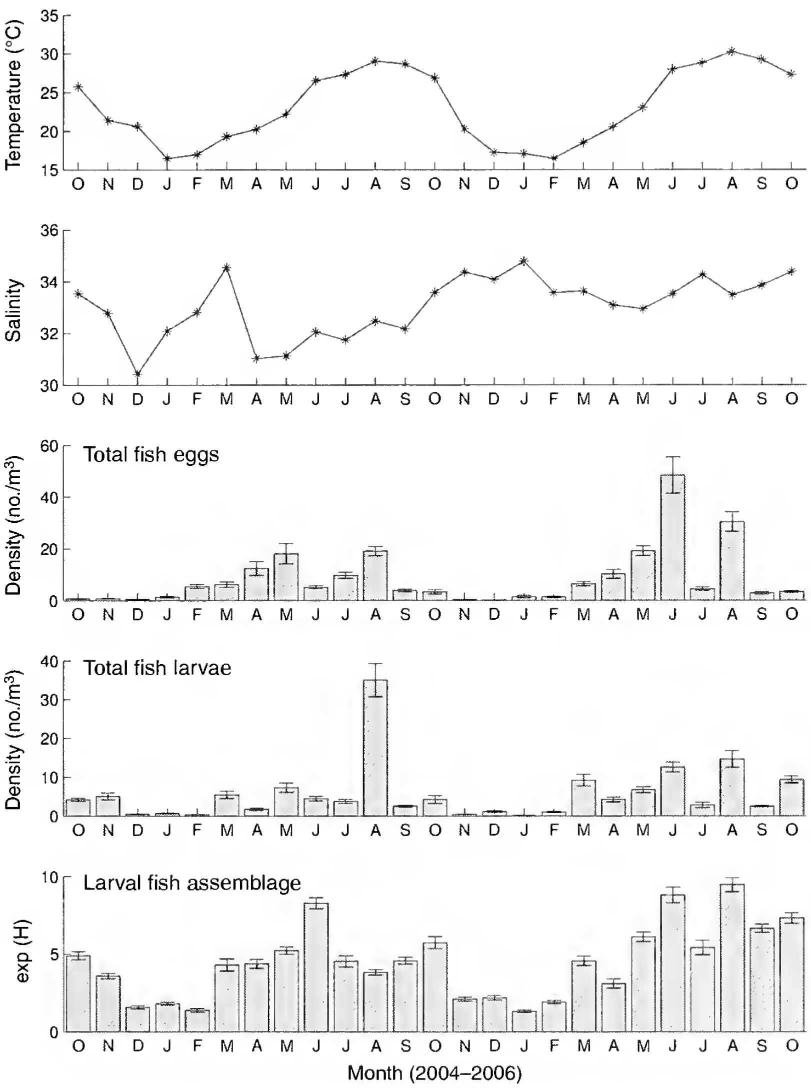


Figure 3

Mean temperature and salinity, fish egg and larval fish concentrations, and diversity indices for larval fish assemblages for October 2004–October 2006. Temperature and salinity are depth-integrated mean values for each month. Egg and larval fish concentrations are standardized by volume of water filtered (error bars denote ±1 standard error). Calculation of diversity follows Jost (2006) and depicts the exponential function of Shannon entropy, *H* (error bars denote ±1 standard error).

Discussion

Although numerous ichthyoplankton surveys have been conducted in the northern Gulf of Mexico, most have been conducted off the coasts of Texas, Louisiana, and Florida (Ditty et al., 1988), and few have been conducted with a high level of temporal resolution and sample replication. The Alabama shelf region, although relatively small, is unique in that it is bounded by two major topographic features (Mississippi River Delta to the west and DeSoto Canyon to the east) that potentially inhibit alongshore transport of larvae (Johnson et al., 2009). In addition, the Alabama continental shelf receives freshwater outflow from the Mobile River system, which drains the fourth largest watershed in the United States and has the sixth largest freshwater discharge on the North American continent (Park et al., 2007). As a result, the inner shelf environment off Alabama is a highly productive region that supports valuable

Table 3

Summary (90% cumulative percentage and abundance ranking) of the dominant family groups collected during the 2004–2006 ichthyoplankton survey in the northern Gulf of Mexico off the coast of Alabama and from other ichthyoplankton surveys in the general vicinity.

	This study	ENTRIX (2006)[1]	Rakocinski et al. (1996)[2]	Williams (1983)[3]
Family	% (Rank)	% (Rank)	% (Rank)	% (Rank)
Engraulidae	50.5 (1)	32.3 (1)	82.0 (1)	69.3 (1)
Sciaenidae	15.9 (2)	10.2 (3)	4.0 (3)	14.0 (2)
Carangidae	5.4 (3)	2.7 (8)	5.0 (2)	2.8 (4)
Clupeidae	5.0 (4)	15.5 (2)		4.3 (3)
Paralichthyidae	3.9 (5)	8.5 (4)		
Gobiidae	3.6 (6)	4.1 (6)		
Ophidiidae	2.5 (7)	3.6 (7)		
Cynoglossidae	2.1 (8)	5.6 (5)		
Synodontidae	0.9 (9)	1.9 (9)		
Triglidae	0.8 (10)	0.8 (13)		
Serranidae		1.9 (10)		
Bregmacerotidae		1.6 (11)		
Labridae		1.0 (12)		
Callionymidae		0.7 (14)		
Stromateidae		0.4 (15)		
Scombridae		0.3 (16)		
Lutjanidae		0.2 (17)		
Congridae		0.2 (18)		
Ophichthidae		0.2 (19)		
Tetraodontidae		0.2 (20)		
Cumulative %	90.6	91.9	91.0	90.4

[1] Samples (oblique) were collected as part of the SEAMAP ichthyoplankton survey (Rester el al., 2000) during the months of June–November from 1982 to 2002 by using a 61-cm bongo net fitted with 333-μm mesh. Sample stations were limited to the Mississippi and Alabama inner-shelf region.

[2] Samples (upper and lower water column) were collected monthly from November 1979 to October 1980 in Mississippi Sound by using a 1-m diameter opening-closing conical-ring plankton net with 335-μm mesh.

[3] Samples (surface and demersal) were collected monthly from March 1979 to February 1980 in lower Mobile Bay by using a 1×0.5-m rectangular opening plankton net with 505-μm mesh.

fisheries resources (Shipp, 1992). The establishment of our survey is the first to specifically target larval fish assemblages in Alabama shelf waters and is the only survey from the northern Gulf of Mexico to combine frequent sampling effort (monthly) with high temporal replication (64+ samples/month) for a relatively long duration (25 months). Few ichthyoplankton surveys have been conducted near our sampling location, including a one-year survey of lower Mobile Bay (Williams, 1983), a one year survey of Mississippi Sound (Rakocinski et al., 1996), and a summary of SEAMAP ichthyoplankton data collected on the Mississippi and Alabama shelf during 1982–2002 (ENTRIX, 2006). The fisheries-independent data collected during our survey, therefore, provide a baseline for future comparisons with respect to variability in local oceanographic and climatic features (e.g., warming water temperatures), water and land usage (e.g., Mobile Bay nutrient loading and water outflow), and habitat modifications (e.g., artificial reef programs).

A comparison of results among multiple ichthyoplankton surveys is complicated because the motives for surveys often differ, resulting in survey-specific protocols and sampling biases. For example, the summary of larval fish seasonality reported by Ditty et al. (1988) for the northern Gulf of Mexico included over 30 separate surveys covering a wide range of spatial extent (Gulf-wide to individual bays and passes), sampling depths (neuston to 200 m), mesh sizes (0.086–1.05 mm), gear types (eight different samplers), sampling frequency (biweekly to quarterly), and survey duration (weeks to years). In addition, the taxonomic level to which ichthyoplankton are identified and at which they are reported varies with larval fish size, condition after capture, and availability of adequate descriptions. Our decision to use a 202-μm mesh size (as opposed to more standard sizes, e.g., ≥333 μm) is the factor that most likely biases our survey results when compared with previous studies. The effect of mesh size on the reten-

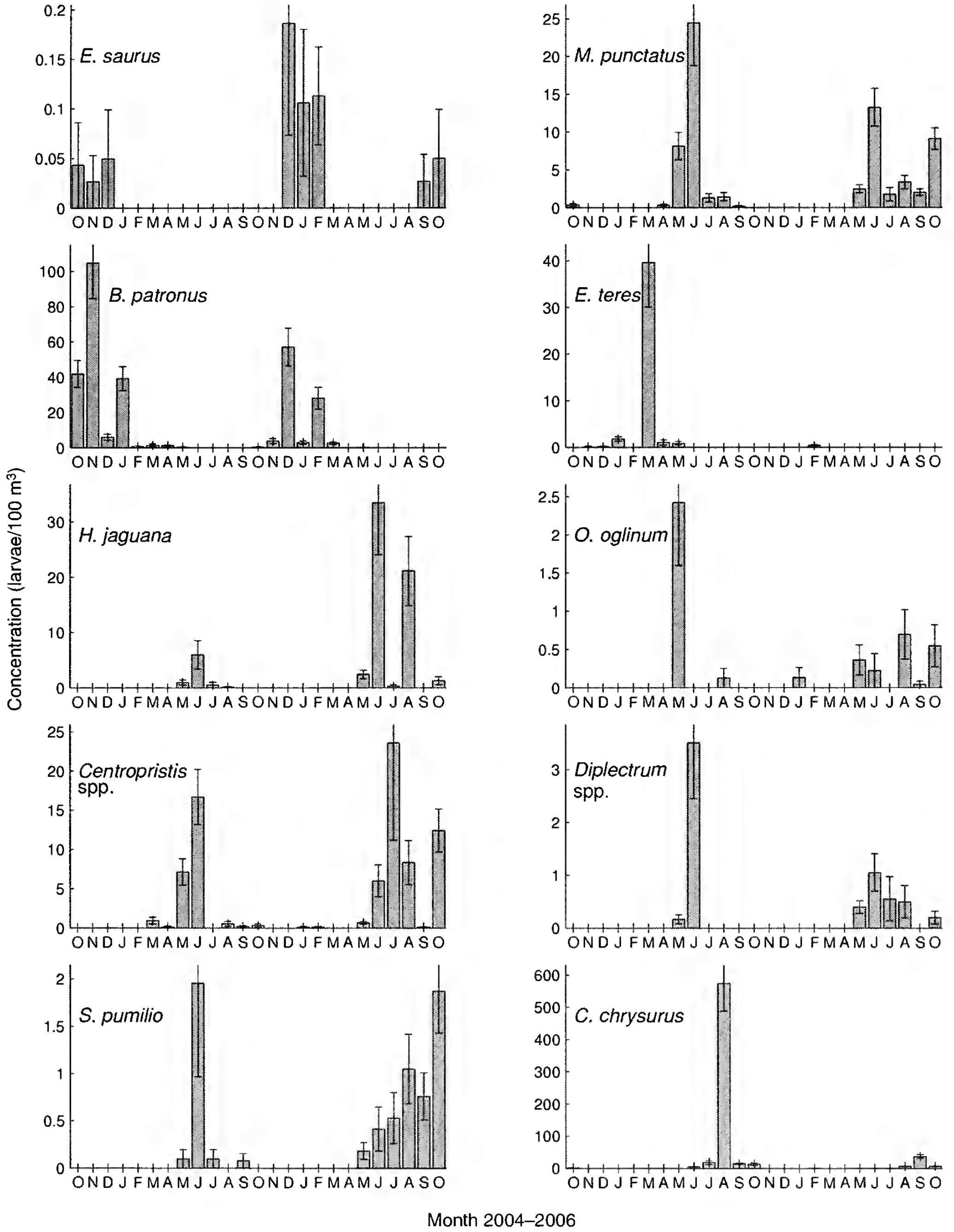
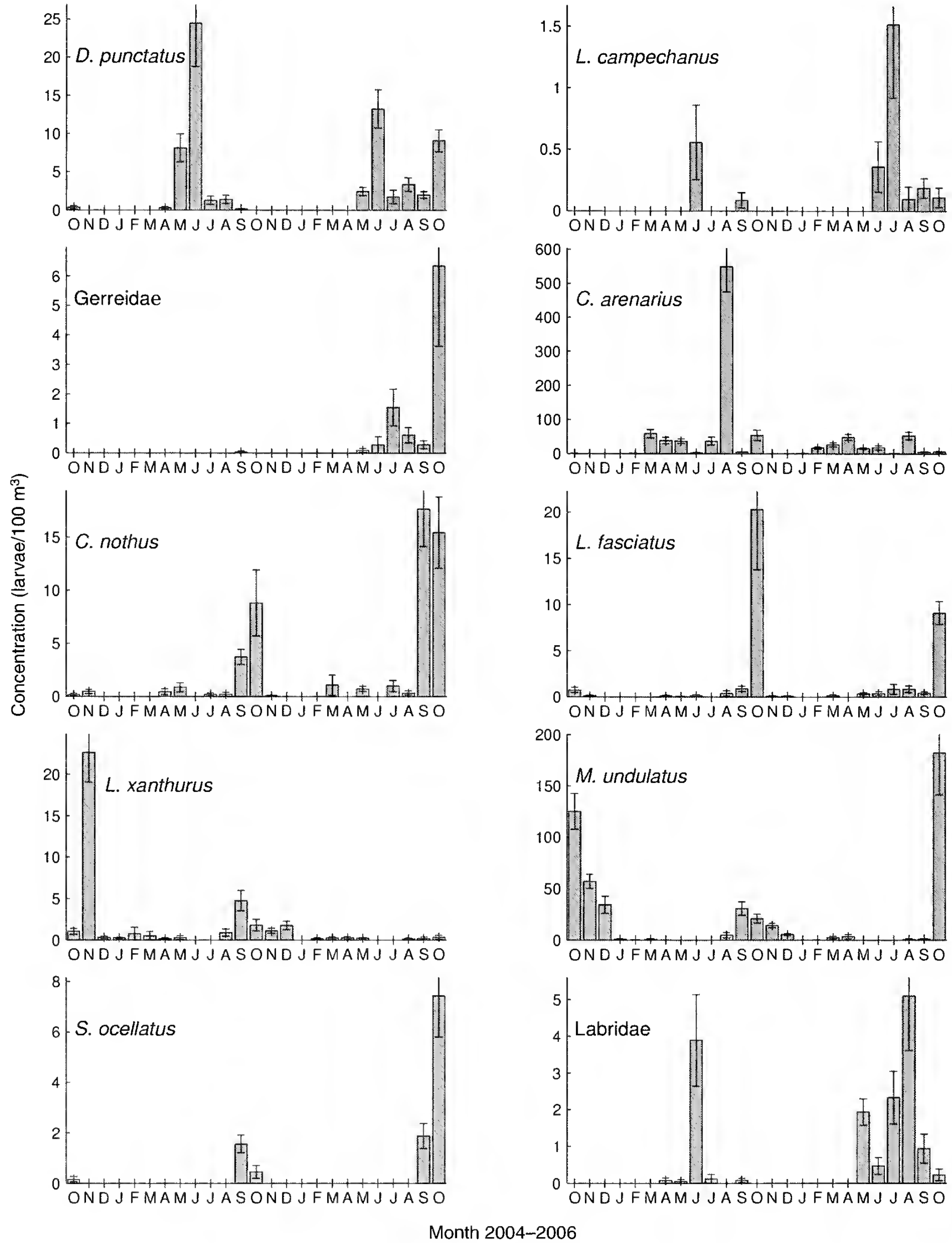


Figure 4

Mean larval concentrations (no./100 m^3) of dominant taxa for each month during the ichthyoplankton survey (October 2004–October 2006). Error bars denote ±1 standard error. Figure panels are presented in taxonomic order, as listed in Table 2.

tion of larvae has been documented in numerous studies, with the general conclusion that larger mesh sizes may efficiently collect the late larval stages but underestimate the smaller size classes because of extrusion (Houde and Lovdal, 1984; Leslie and Timmins, 1989). Conversely, smaller mesh nets may collect smaller size classes of larvae, but are prone to clogging, thus reducing their effectiveness in sampling ichthyoplankton, particularly late-stage fish larvae (Smith et al., 1968; Tranter and Smith, 1968). In our study the smaller mesh size enabled us to achieve better estimates of fish egg and preflexion larval fish concentrations, which



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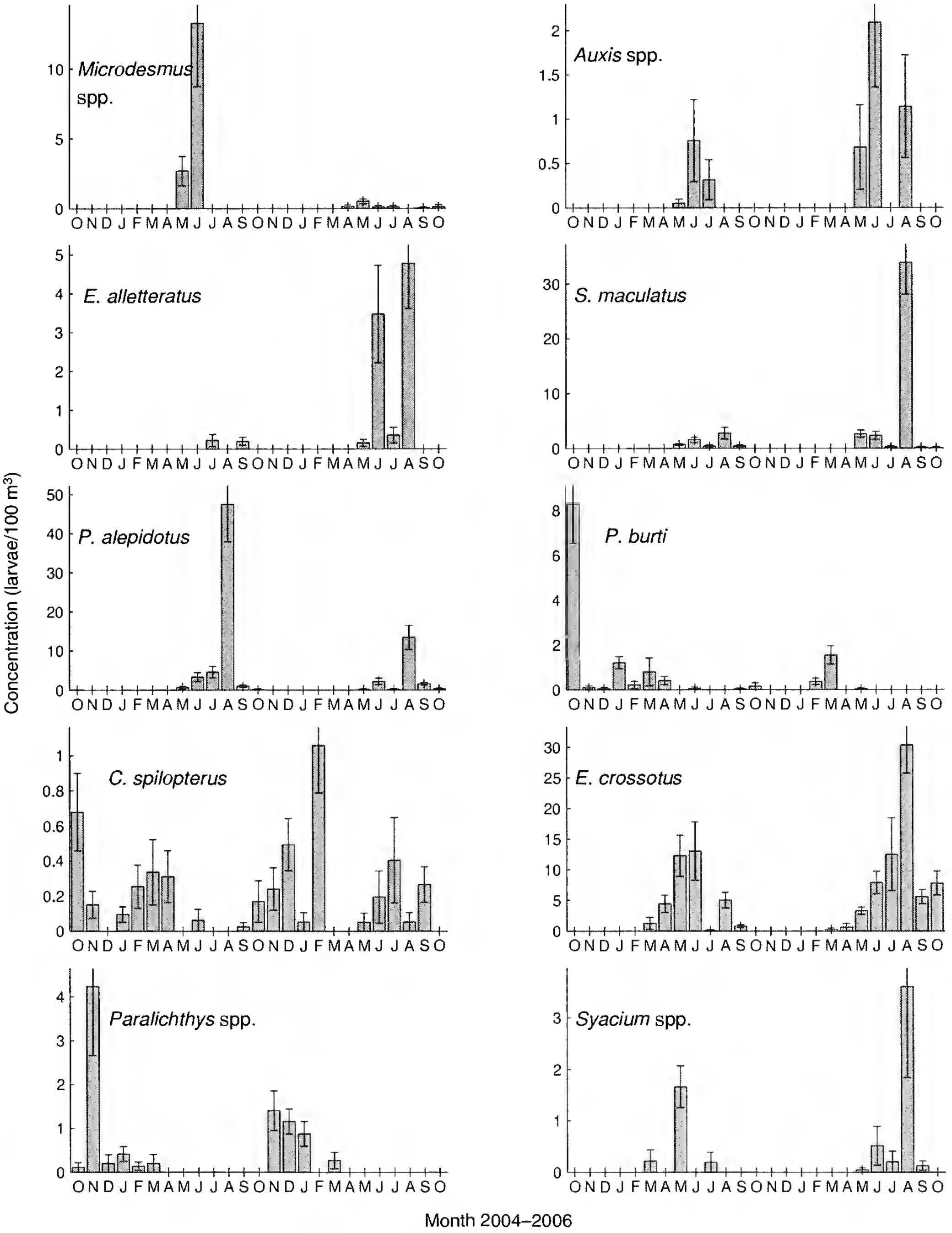
are indicative of nearby adult spawning activity. The tradeoff, however, was that many of the larvae were too small to identify to the genus or species level. As a result, most fish larvae collected in this survey were identified to the order and family level only (14% and 52%, respectively).

Fifty-eight different families of fishes were collected in our ichthyoplankton collections, the adult forms of which represent diverse zoogeographic regions and ecological niches. As expected, larvae of nearshore and inner shelf species were the most dominant, such as coastal pelagic (e.g., engraulids, carangids, clupeids, stromateids, gerreids) and coastal demersal (e.g., sciaenids, paralichthyids, gobiids, cynoglossids, synodontids) species. Unidentified engraulids were the most abundant larval fish group in our survey (ap-



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proximately 50%) and in the aforementioned regional surveys (Table 3). Engraulid larvae appear to be more abundant in protected coastal waters, as indicated by their higher dominance in the surveys of Mobile Bay (82%) and Mississippi Sound (69%), both of which are shallow estuarine regions. On the basis of identification of larger specimens, most of the engraulids collected in Mobile Bay and Mississippi Sound were *Anchoa mitchilli* and *A. hepsetus* (Williams, 1983; Rakocinski et al., 1996), whereas our collections contained these species as well as the coastal species *A. nasuta* and *Engraulis eurystole*. The inner shelf taxa *Brevoortia patronus*, *Cynoscion arenarius*, *Micropogonias undulatus*, *Chloroscombrus chrysurus*, and unidentified gobies were among the most dominant ichthyoplankton in all surveys, including ours. As adults, these fishes are ex-

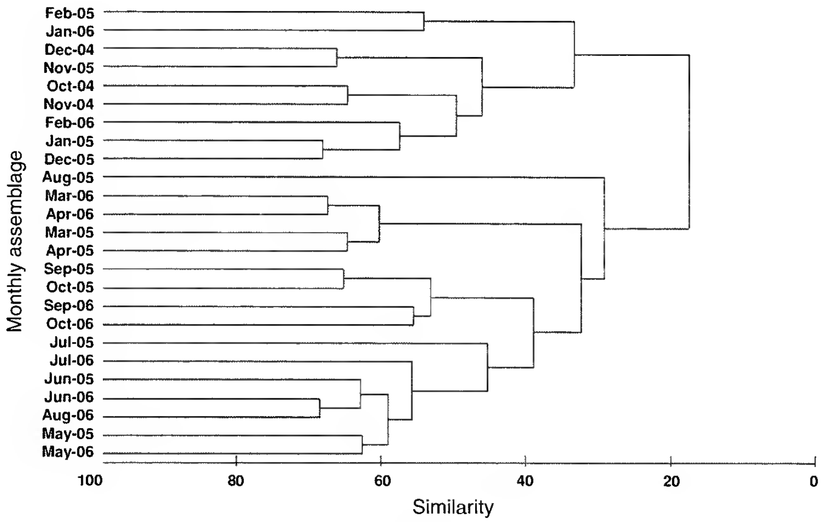

Figure 5

Dendrogram depicting relationships (based on Bray Curtis similarities) of the dominant taxonomic assemblages between months. Larval concentrations for dominant taxa were square-root transformed before analyses.

tremely abundant in estuarine and inner shelf waters and serve important ecological roles as forage fishes (e.g., *B. patronus*, *C. chrysurus*) and as predators linking primary consumers to higher trophic levels (e.g., *M. undulatus*, *C. arenarius*) (Naughton and Saloman, 1981; Overstreet and Heard, 1982; Sheridan et al., 1984; Franks et al., 2003). The larvae of these relatively few taxa often comprise the majority of ichthyoplankton in surveys throughout the northern Gulf of Mexico (Ditty, 1986; Cowan and Shaw, 1988; Tolan et al., 1997).

Flatfish larvae (e.g., paralichthyids and cynoglossids) represented another dominant coastal group. Cynoglossids (*Symphurus* spp.) were common year-round in our study, which indicates that our collections contained multiple species. These fishes are commonly reported in ichthyoplankton surveys throughout the Gulf of Mexico, but identification of larvae (and adults) is problematic owing to high species richness and overlapping meristics (Farooqi et al., 2006b). Similarly, *Citharichthys* spp. were abundant year-round, as were *C. spilopterus*. Again, identification down to species is problematic because five species (*C. arctifrons*, *C. cornotus*, *C. gymnorhinus*, *C. macrops*, and *C. spilopterus*) are found in the study region (Lyczkowski-Shultz and Bond, 2006). Although efforts were made to identify larvae conservatively, some of our *C. spilopterus* may have included congeners. This issue of questionable identification appears less likely for the *Etropus* species complex, which was also abundant, primarily *E. crossotus* and *E. microstomus*.

Equally notable in our survey was the absence (or rarity) of larvae from taxa that are common in our sampling region as adults. For example, serranine (seabasses) serranid larvae were collected, but epinepheline (grouper) larvae were not. Similarly absent (or rare) were larvae from other recreational and commercially important species such *Coryphaena hippurus* (Coryphaenidae), *Rachycentron canadum* (Rachycentridae), *Balistes capriscus* (Balistidae), *Lobotes surinamensis* (Lobotidae), *Chaetodipterus faber* (Ephippidae), and *Mugil cephalus* (Mugilidae), all of which spawn in coastal or offshore waters of Alabama. The fact that we did not collect some of these taxa is not surprising (e.g., *B. capriscus*, *M. cephalus*) because they are more commonly collected in the neuston (which we did not sample). The absence of grouper larvae is perplexing, even though the rarity of epinepheline larvae has been documented in the northern Gulf of Mexico. For example, only 37 grouper larvae were collected in gulf-wide SEAMAP ichthyoplankton surveys between 1982 and 1999 (>7000 samples) (Lyczkowski-Shultz et al.[1]). Most of the grouper larvae were collected at offshore SEAMAP sampling stations, which indicates that their occurrence in nearshore environments may be rare. It is possible that the limited spatial extent of our survey (i.e., a single station) may have influenced our estimates of larval fish concentrations and variability, because coastal marine processes that influence larval fish dynamics are often site-specific (e.g., local wind regimes, tidal flows, river discharge), but the overall seasonal supply of larvae available at our sampling station is likely representative of the ichthyofauna from a larger northcentral Gulf of Mexico region between the 87°W and 89°W longitude (Boschung, 1992).

The main objective of this study was to describe taxon-specific seasonality for larval fishes collected in the survey region. For several reasons, we limited our seasonal analyses to water temperature, as opposed to a suite of environmental parameters. First, temperature has long been proposed as an important factor in the initiation of spawning for marine fishes (Orton, 1920), and numerous field and laboratory (primarily aquaculture-related) studies have provided support for temperature as a primary influence (Arnold et al., 2002; Sheaves, 2006). Second, water temperature varies predictably at seasonal scales (e.g., months), as opposed to other factors that vary at shorter time scales. Our salinity data (Fig. 3), for example, showed no seasonal trends and were not correlated with egg or larval fish concentrations. The monthly mean salinity values calculated during each cruise likely reflect short-term variability related to tidal flow, riverine outflow, local wind conditions, and related factors that affect salinity at our sampling station. In addition, salinity, although an important factor for many estuarine-spawning species, is generally considered less important than temperature to the timing of marine fish spawning (Bye, 1984; Sheaves, 2006).

Defining seasonality in terms of water temperature also provides a framework for monitoring fisheries dynamics with respect to anticipated rises in sea temperature due to global climate change. Our monthly observed depth-integrated temperatures were relatively consistent with those for the previous ten-year average for the region, although winter (December–January) and late summer (August–October) values were generally higher (Fig. 2). Fodrie et al. (2009) noted a significant increase in sea surface temperature near the mouth of Mobile Bay over a 20-year period (1987–2007). The authors also noted a concurrent increase in the number and occurrence of juvenile subtropical and tropical fishes collected in seagrass meadows along the northern Gulf of Mexico. For example, in 2006–2007 surveys, juveniles of tropical species such as *Chaetodon ocellatus* (Chaetodontidae), *Fistularia tabacaria* (Fistularidae), *Ocyurus chrysurus* (Lutjanidae), *Thalassoma bifasciatum* (Labridae), *Sparisoma viride* (Scaridae), and unidentified acanthurids were collected in coastal habitats where they were not collected during previous surveys (1971–79) (Livingston, 1985). Notably, in our ichthyoplankton survey larvae from all of these families, except Chaetodontidae, were collected but regrettably, comparable ichthyoplankton data from the 1970s were not available and our identifications were made only to the family level.

Conclusions

Increases in regional water temperatures may have significant impacts on the reproductive success of marine fishes and the subsequent survival of early life stages, including early gonad maturation and spawning in adults, altered larval transport pathways, extended pelagic larval durations, changes in larval assemblage structure, and mismatched timing of larval fish occurrence with food resources and physiological optima, among other effects (Sheaves, 2006; O'Conner et al., 2007; Genner et al., 2009). Establishment of long-term baseline surveys provides a means of monitoring larval fish assemblages and the factors that influence larval fish dynamics in order to provide early indicators of ecosystem changes due to environmental perturbations. The ichthyoplankton survey efforts described here for the October 2004–October 2005 period have since continued and expanded to include near monthly (depth-discrete) ichthyoplankton sampling at five stations along a cross-shelf transect from inside Mobile Bay extending offshore to a station approximately 54 km south of Dauphin Island. The expanded survey program (Fisheries Oceanography of Coastal Alabama, or FOCAL) will allow us to estimate and monitor the variability in ichthyoplankton seasonality, abundance, assemblage structure, and vertical distribution over multiple temporal and spatial scales.

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Observer-reported skate bycatch in the commercial groundfish fisheries of Alaska

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Abstract—We analyzed skate catch data collected by observers in the North Pacific Groundfish Observer Program (NPGOP) from 1998 through 2008 to document recent changes in the identification of skates by observers and to examine the species composition of observed skate catch in Alaska's groundfish fisheries as well as recent trends in skate retention by commercial fishermen. Historically, almost all skate bycatch has been reported by NPGOP observers as "skate unidentified." However, since 2004 observers have been trained to identify skates to the genus and species level. In 2008 over 95% of all skates were identified at least to the genus level, and over 50% were identified to species. The most common species of skates identified by observers in groundfish fisheries are *Bathyraja parmifera* (Alaska skate), *Raja binoculata* (big skate), and *Bathyraja aleutica* (Aleutian skate). Species composition of reported skate catch generally reflects recent survey-derived biomass estimates, with *B. parmifera* dominating the catches in the Bering Sea and, to a lesser extent, in the Aleutian Islands region, and species of the genus *Raja* dominating catches in the Gulf of Alaska. A relatively high percentage of the skate catch on longline vessels is still reported at the family or genus level because of difficulties in the identification of skates not brought onboard the vessel. For the larger skate species, the proportion retained for processing has increased in recent years as the market price for skate product has increased. Although observed skate catch does not give a complete account of skate bycatch in the fisheries of the region, observer data provide critical information for the appropriate management of skate populations in Alaska.

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Skates are large, long lived fishes with relatively slow growth rates and low reproductive potential (Ebert, 2005; Ebert et al., 2008). These aspects of their life history, combined with their relatively low mobility and benthic habitat, make skates particularly vulnerable to fishing pressure and slow their recovery from population declines; yet few countries have management plans for skates or other chondrichthyan species (Stevens et al., 2000). In cases where skates are targeted by fisheries, population declines can be rapid (Agnew et al., 2000). Moreover, because discard mortality can be high (Stobutzki et al., 2002; Laptikhovsky, 2004), skate populations may be dramatically affected by fishing activity even if they are not targeted directly (Brander, 1981; Casey and Myers, 1998; Dulvy et al., 2000; Stevens et al., 2000). In addition to population declines, fishing pressure may lead to significant shifts in community structure because declines in some species of a skate assemblage may be masked by increases in other, more resilient species (Agnew et al., 2000; Dulvy et al., 2000; Stevens et al., 2000). Therefore, effective management of skate populations requires species-specific data on abundance trends and exploitation rates.

Skates are regularly caught in nearly all of the commercial groundfish fisheries currently prosecuted in Alaska waters, including fisheries targeting Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), yellowfin sole (*Limanda aspera*), and other species (Ormseth et al., 2009). In addition to their ubiquitous presence as bycatch species, skates have been targeted in Alaska waters on a short-term regional basis. An unregulated fishery targeting *Raja binoculata* (big skate), *R. rhina* (longnose skate), and assorted species of *Bathyraja* (including Alaska skates) developed in the central Gulf of Alaska (GOA) in February 2003. Shifting economic conditions and fishing seasons soon made other target species more valuable, but this short-lived fishery revealed that skates can quickly become an attractive alternative target when other fisheries are closed (Matta, 2006). More recently, the Alaska Department of Fish and Game (ADF&G) approved a pilot fishery for big and longnose skates in the state-managed waters of Prince William Sound (ADF&G Emergency Order #2-G-E-04-09) in 2009. Elsewhere in Alaska skates are still managed as part of a large nontarget species complex, although beginning in 2011 skates in the Bering Sea and Aleutian Islands will be managed as a separate unit.

Recent advances in the taxonomy of the skates of the North Pacific and Bering Sea (Ishiyama and Ishihara, 1977; Ishihara and Ishiyama, 1985, 1986; Stevenson et al., 2004, 2007, 2008) have facilitated increasingly detailed identification of skates by observers in the commercial fisheries of Alaska. The resulting wealth of detailed catch data now permits an examination of skate bycatch on a level that was not previously possible. The objectives of this study are 1) to document recent changes for the identification of skates in the NPGOP, and 2) to provide an overview of potential management concerns by examining the species composition of observed skate catch (OSC) in Alaska's groundfish fisheries and recent trends in skate retention by commercial fishermen.

Materials and methods

All data used for this study were extracted from the North Pacific Groundfish Observer Program (NPGOP) database maintained by the Fisheries Monitoring and Analysis (FMA) Division of the National Marine Fisheries Service's (NMFS) Alaska Fisheries Science Center. This database houses all biological data collected by groundfish observers onboard commercial fishing vessels operating in the waters of Alaska's federal Exclusive Economic Zone (EEZ). For an overview of the database, see the FMA Division website (National Marine Fisheries Service, http://www.afsc.noaa.gov/FMA/fma_database.htm, accessed November 2009).

Federal law requires observers to be present at all times on commercial fishing vessels of 125 ft (38.1 m) or more in length overall (LOA) operating in the federal EEZ. For vessels from 60 to 124 ft (18.3 to 37.8 m) LOA, observer coverage is required for only 30% of fishing days and for vessels less than 60 ft (18.3 m) LOA no observer coverage is required. The catch data used for this study were taken from trawl hauls and longline sets during which an observer was present and was sampling, so that the catch statistics presented here do not represent the total catch of the fisheries in this region, nor do they represent biomass estimates. For some commercial fisheries in the area, pot gear is used, but observers rarely encounter skates in these fisheries, and therefore such data are not included in this study.

The process used by observers to determine the species composition and catch weights of sampled hauls depends on gear type. Observers on trawlers may determine the species composition of a haul by identifying and weighing the entire catch, which is usually not possible, or by choosing a random sample (generally 300 kg or more) of the catch and identifying and weighing all taxa within the sample. The proportion by weight of each taxon in the sample is then extrapolated to the total catch weight, which may be determined by a number of methods, including flow scale readings, codend measurements, or bin volume estimates. On longline vessels, observers randomly select a "tally period" as the gear is being retrieved. During this tally period, the observer identifies and counts specimens, including specimens that drop off the line or are intentionally discarded. A subset of the specimens identified during the tally period (15 or more per species, when possible) is retained onboard the vessel and weighed to determine an average weight for each taxon. That average weight is then applied to all specimens identified during the tally period, and the resulting proportional species composition is extrapolated to the total gear set to obtain a total catch weight for each species for each set. The basic data unit used for this study is the extrapolated catch weight for each taxon from each observed haul or set (hereafter trawl hauls and longline sets will be collectively referred to as "hauls"). The total observed skate catch (OSC) was calculated by summing extrapolated catch weights for all skate taxa (including the following unidentified skate groups: "skate unidentified," "*Bathyraja* sp.," and "*Raja* sp.") across all hauls in which skates were identified. Scientific and common names for skate taxa follow Stevenson et al. (2007).

From the inception of the NPGOP through the sampling year 2002, observers were not trained to identify skates and were therefore not required to identify them beyond the family level. During 2002 and 2003, a field identification key was developed (Stevenson, 2004) and experienced observers began receiving training in skate identification during annual briefings. Feedback from experienced observers was used to refine the identification materials and classroom training, and beginning with the 2004 sampling year, all new and returning observers were provided with skate identification training and materials for identification of skate in the field. Since 1 January 2004 all observers have been required to identify skates to the species level when possible. Because of these changes in observer identification training and policies, two separate but overlapping time frames were used in this study. To investigate the trends in observed skate catch and the history of skate identification by observers an 11-year time frame was chosen and queries were restricted to data collected from 1 January 1998 through 31 December 2008. For investigations of species-level trends in observer data, queries were restricted to data collected from 1 January 2004 through 31 December 2008—a period that corresponds with the time period in which all new and returning observers have been trained to identify skates to the species level. Regions were defined on the basis of NMFS management areas: Bering Sea comprises the Bering Sea NMFS management areas 509–524; the Aleutian Islands region comprises NMFS management areas 541–543; and the Gulf of Alaska comprises NMFS management areas 610–650 (Fig. 1). All catch proportions are presented as a percentage of total observer reported catch weight.

The targeted resource was not directly recorded in observer catch data, so that for the purposes of this study, the term "target species" is defined as the predominant species in the catch. "Predominant species" was defined as the species accounting for the highest percentage of the extrapolated weight in the species composition sample and was determined on a haul-by-haul basis. Percent retained data are subjective estimates made by observers using visual approximations, along with information provided by the vessel's captain or factory manager. Mean retention rates used here are weighted averages calculated annually for each species with the following equation:

$$\frac{\sum_j R_{ij} C_{ij}}{\sum_j C_{ij}},$$

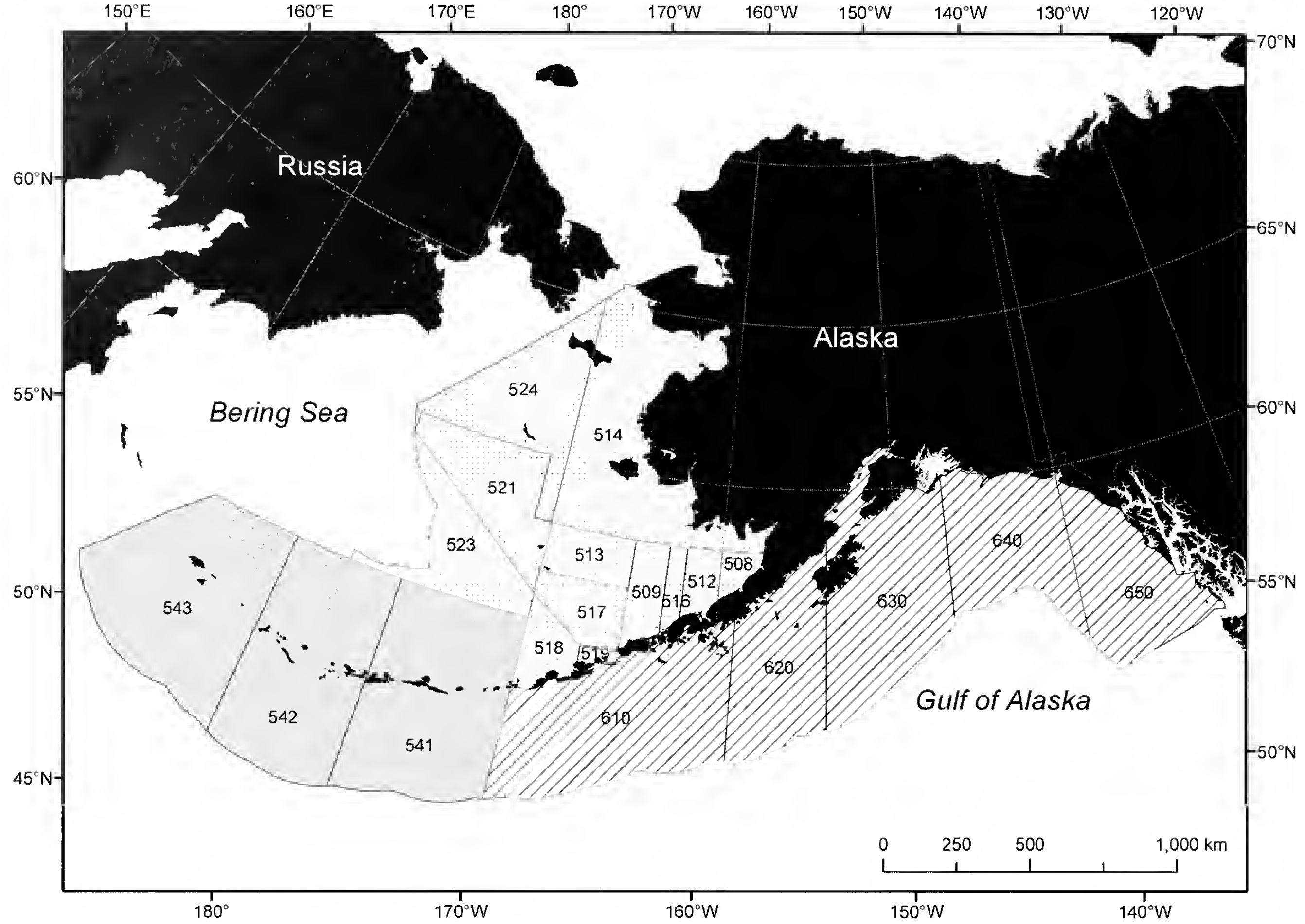

Figure 1

Map showing NMFS management areas in which observed skate catch was examined from 1998 through 2008. Stippled areas=Bering Sea, shaded areas=Aleutian Islands, diagonal hatching=Gulf of Alaska.

where R_{ij} = the observer reported retention rate of species i in haul j; and

C_{ij} = the extrapolated catch weight of species i in haul j.

Historical skate price information was derived from Alaska state fish-ticket data, and was compiled for the study period by Terry Hiatt (unpubl. data[1]). An annual mean price was determined for each taxon by 1) calculating the exvessel price paid per pound round weight at each delivery to all processors where the purchase of raw skates from Alaska waters was recorded, and then 2) calculating the simple average of those delivery price points over the calendar year. Round weight refers to intact whole specimens. For deliveries consisting of nonwhole specimens, round weight (in pounds) was calculated from net delivery weight by using a product recovery rate (PRR) of 0.32 for "wings" and 0.9 for gutted animals (National Marine Fisheries Service, http://www.fakr.noaa.gov/rr/tables/tabl3.pdf, accessed November 2009). Each annual mean represents at least 334 (range: 334–2247) data points.

Results

Skate species composition reported by observers over the past decade has changed considerably. Up to and including 2002, over 98% of OSC was reported as "skate unidentified" (Table 1). In 2003, less than 90% of OSC was unidentified, and the proportion of unidentified skates has continued to drop through 2008, a year in which only 2% of OSC was unidentified. Because the proportion of unidentified skates has dropped, the proportions of skates identified to the genus level (*Bathyraja*) and to the species level (*Bathyraja parmifera*, *Raja binoculata*, etc.) have continued to rise. In 2008, 46% of OSC was identified to the genus level and approximately

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[1] Hiatt, T. 2009. NMFS Alaska Fisheries Science Center, Seattle, WA 98115.

Table 1

Species composition (% by weight) of observed skate catch by year reported in Alaska's groundfish fisheries for 1998–2008. * = less than 0.1%.

Taxon	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2004–2008
Skate unidentified	99.7	99.6	99.5	98.6	98.6	88.7	61.3	25.2	21.4	7.1	2.4	23.2
Bathyraja sp.	*	*	0.1	1.1	0.2	0.4	0.5	39.3	34.2	42.6	47.4	33.1
Bathyraja parmifera (Alaska skate)	*	*	0.1	0.2	0.7	7.9	30.2	27.2	36.6	40.0	40.1	34.8
Bathyraja aleutica (Aleutian skate)	*	*	*	*	0.1	0.7	2.2	2.6	1.9	2.5	2.7	2.4
Bathyraja interrupta (Bering skate)	*	*	*	*	*	0.3	1.6	1.5	1.1	1.3	2.7	1.7
Bathyraja maculata (whiteblotched skate)	*	*	*	*	*	0.1	1.1	0.4	0.7	0.5	1.0	0.7
Bathyraja lindbergi (Commander skate)	*	*	*	*	*	*	0.1	0.2	0.1	0.2	0.2	0.2
Bathyraja taranetzi (mud skate)	*	*	*	*	*	*	0.2	0.1	*	0.1	0.3	0.2
Bathyraja trachura (roughtail skate)	*	*	*	*	*	*	0.1	*	0.1	0.1	*	0.1
Bathryaja minispinosa (whitebrow skate)	*	*	*	*	*	*	*	*	*	*	*	*
Raja sp.	*	*	*	*	*	*	*	0.1	0.5	*	0.1	0.1
Raja binoculata (big skate)	0.3	0.4	0.3	*	0.2	1.7	2.3	2.3	2.4	3.7	2.1	2.5
Raja rhina (longnose skate)	*	*	*	*	*	0.2	0.5	1.0	1.0	1.9	1.0	1.1

52% was identified to species (i.e., *Bathyraja parmifera* and other species).

The portion of the OSC that was identified to the species level was dominated by *Bathyraja parmifera*, *Raja binoculata*, and *Bathyraja aleutica* (Aleutian skate), which accounted for 40.1%, 2.1%, and 2.7%, respectively, of OSC in 2008 (Table 1). These proportions have remained relatively stable since observers began identifying skates in 2004, with *B. parmifera*, *R. binoculata*, and *B. aleutica* averaging 34.8%, 2.5%, and 2.4%, respectively, of the annual OSC from 2004 through 2008. Seven other species of skates, including *R. rhina* and six species of *Bathyraja* (*B. interrupta*, *B. maculata*, *B. lindbergi*, *B. taranetzi*, *B. trachura*, *B. minispinosa*), have been regularly reported in smaller proportions by observers since 2004. Although unidentified skates now constitute less than 5% of OSC, a large proportion of skates are still identified only to the genus level ("*Bathyraja* sp." and "*Raja* sp.").

The species composition of OSC varied by region and by gear type within each region. During the 2004–08 period, *Bathyraja parmifera* was the most commonly observed species in both the Bering Sea and Aleutian Islands region (Table 2). In the Bering Sea, no other single species made up more than 1.7% of OSC, and a large percentage of skates were identified only to the genus level. Species composition profiles were similar for both types of trawl, but for fisheries using longline gear a much higher percentage of skates were not identified to the species level.

In the Aleutian Islands, *B. parmifera* again accounted for a higher proportion of OSC than any other species (Table 2). However, notable proportions of *B. maculata* and *B. aleutica* were reported in this region as well. As in the Bering Sea, a large proportion of the skates were not identified to the species level, and most of the unidentified skates and skates identified to genus were encountered in fisheries using longline gear. The species composition profile for pelagic trawl gear in the Aleutian Islands, with only two species reported and *B. interrupta* accounting for over 80% of OSC, was markedly different from any of the other region-gear combinations reported in our study. However, that profile was based on only two species composition samples in which skates were reported.

The species composition of OSC was quite different in the Gulf of Alaska, where the two species of *Raja* (*R. binoculata* and *R. rhina*) are more common, accounting for over half of OSC in the region (Table 2). Among species of *Bathyraja*, *B. aleutica* accounted for the highest proportion in the Gulf of Alaska. The proportion of skates not identified to the species level was considerably lower in the Gulf of Alaska than in either the Bering Sea or Aleutian Islands, and the species composition

Table 2

Species composition (% by weight) of observed skate catch by region and by gear type within each region of Alaska for 2004–2008. Regions: BS=Bering Sea, AI=Aleutian Islands, GOA=Gulf of Alaska. Gear types: 1=Nonpelagic trawl, 2=Pelagic trawl, 3=Longline. * = less than 0.1%.

	BS				AI				GOA			
Taxon	1	2	3	All	1	2	3	All	1	2	3	All
Skate unidentified	0.6	1.4	33.5	24.2	3.9	*	25.1	17.6	2.4	3.5	16.7	9.6
Bathyraja sp.	1.9	1.5	47.5	34.5	4.7	*	40.7	28.0	2.2	3.3	16.5	9.4
Bathyraja parmifera	90.0	92.8	14.9	36.6	50.9	*	18.0	29.6	3.6	9.4	2.8	3.2
Bathyraja aleutica	3.0	2.4	1.2	1.7	16.1	*	3.7	8.0	9.5	9.8	13.7	11.6
Bathyraja interrupta	1.3	1.3	1.7	1.6	1.1	80.6	0.4	0.7	5.9	6.3	3.0	4.4
Bathyraja minispinosa	0.1	*	*	*	0.1	*	0.1	0.1	*	*	*	*
Bathyraja maculata	0.4	*	0.2	0.2	17.2	*	9.3	12.1	*	*	0.2	0.1
Bathyraja lindbergi	*	*	0.1	0.1	0.2	*	1.7	1.1	*	*	0.2	0.1
Bathyraja taranetzi	0.2	0.1	*	0.1	5.2	19.4	0.6	2.2	*	*	*	*
Bathyraja trachura	*	*	*	*	0.1	*	0.2	0.2	*	*	1.4	0.7
Raja sp.	*	*	*	*	*	*	*	*	0.6	0.3	4.6	2.6
Raja binoculata	2.4	0.4	0.7	1.0	0.4	*	0.2	0.3	52.3	24.8	19.6	35.7
Raja rhina	0.1	*	*	*	*	*	*	*	23.4	42.6	21.3	22.4
Total	100	100	100	100	100	100	100	100	100	100	100	100

profiles varied more by gear type than in the other two regions. All three gear types were dominated by species of *Raja*, but *R. binoculata* accounted for over 50% of OSC from nonpelagic trawl gear, whereas *R. rhina* was the dominant species in pelagic trawl and longline gear. As in the other two regions, proportions of unidentified skates were much higher on longliners than on vessels with other gear types, although a much higher percentage of skates were identified to the species level even with longline gear in the Gulf of Alaska.

Significant amounts of skate bycatch were encountered by observers in fisheries targeting a variety of commercial groundfish species, including Pacific cod, walleye pollock, Atka mackerel, shallow-water flatfishes (primarily yellowfin and rock soles), and others. During the 1998–2008 study period, nearly 72% of OSC was reported in longline fisheries, and over 65% was reported in longline hauls targeting Pacific cod (Table 3). Nonpelagic trawl fisheries accounted for only 22% of OSC, most of which was reported in hauls targeting miscellaneous flatfishes. Pelagic trawl fisheries, essentially all of which target walleye pollock, accounted for very little of OSC (6%). These results reflect the percentages for the Bering Sea, a region in which over 90% of OSC was reported. In the Aleutian Islands significant numbers of skates were also encountered on trawlers targeting Atka mackerel, and in the Gulf of Alaska on trawlers targeting deepwater flatfishes (arrowtooth flounder and Greenland turbot).

The percentage of OSC retained by commercial fishermen has increased over the past decade (Fig. 2). In 1998, overall mean skate retention was just over 12%, and that figure steadily increased to a peak of nearly 40% in 2003. For the most recent 4 years (2005–08) overall skate retention has remained relatively consistent at around 30–35%. Species-level retention data were erratic from 1998 through 2003. They have become more stable since 2004 when observers began consistently identifying skates to the species level, but the annual mean retention for some of the species, particularly the genus *Raja*, still appears relatively inconsistent from year to year. Since 2004, the largest species of skates (*Raja binoculata*, *R. rhina*, *Bathyraja parmifera*, *B. aleutica*, and *B. maculata*) have generally been retained at 30% of OSC or above, and smaller species, such as *B. interrupta*, *B. lindbergi*, *B. taranetzi*, and *B. minispinosa*, have been retained at lower levels (5–15%).

Discussion

From the inception of the NPGOP through 2003, field identification tools for the skates of Alaska were limited, and skate bycatch data were collected at a very basic level. Almost all skates were reported by observers as "skate unidentified." However, from 2004 through 2008 this situation changed rapidly. With the development and deployment of a field guide and the implementation of an observer training protocol (Stevenson, 2004), the proportion of skates identified to the species level has increased dramatically. For the last year included in this study, over 95% of OSC was identified at least to genus, and that proportion may continue to rise in future years

Table 3

Observed skate catch (in tons) by region, gear type, and target species reported in Alaska's groundfish fisheries for 1998–2008. Target species is defined as the predominant species (by % weight) in the catch. * = less than 100 tons.

	Target species									
Region Gear type	Pacific cod (*Gadus macrocephalus*)	Misc. flatfishes	Walleye pollock (*Theragra chalcogramma*)	Arrowtooth (*Atheresthes stomias*) or Turbot (*Reinhardtius hippoglossoides*)	Pacific halibut (*Hippoglossus stenolepis*)	Atka mackerel (*Pleurogrammus monopterygius*)	Rockfishes (*Sebastes* sp.)	Sablefish (*Anoplopoma fimbria*)	Other	Total
Bering Sea										
Nonpelagic trawl	2606	18,400	2476	1677	*	*	*	*	1367	26,675
Pelagic trawl	*	*	8912	*	*	*	*	*	*	8967
Longline	90,314	*	206	967	461	*	*	*	2714	94,766
Aleutian Islands										
Nonpelagic trawl	491	*	*	*	*	1021	443	*	*	2067
Pelagic trawl	*	*	*	*	*	*	*	*	*	*
Longline	3850	*	*	256	497	*	*	140	793	5597
Gulf of Alaska										
Nonpelagic trawl	437	756	*	1393	*	*	262	*	448	3445
Pelagic trawl	*	*	*	*	*	*	*	*	*	*
Longline	1486	*	*	*	443	*	*	319	286	2566
All areas										
Nonpelagic trawl	3534	19,177	2563	3123	101	1072	744	*	1823	32,187
Pelagic trawl	*	*	8967	*	*	*	*	*	*	9061
Longline	95,650	*	208	1229	1401	*	*	493	3794	102,929
Total	99,222	19,253	11,738	4366	1504	1077	843	544	5630	144,177

as training methods and identification tools are further refined.

Patterns of species composition in OSC generally parallel recent biomass estimates for regional skate populations derived from bottom trawl surveys. *Bathyraja parmifera* accounts for the large majority of OSC, which is not surprising given that *B. parmifera* is the most abundant species of skate encountered in bottom trawl surveys conducted in Alaska waters (Stevenson et al., 2008). In fact, *B. parmifera* is particularly common on the Bering Sea continental shelf, where its populations make up about 95% of the total skate biomass (Acuna and Lauth, 2008; Lauth and Acuna, 2009) and where commercial fishing effort for walleye pollock, Pacific cod, and flatfishes is concentrated. Many of the other species encountered by observers in the Bering Sea are recorded from fishing activity on the upper continental slope, where *B. aleutica*, *B. maculata*, and *B. interrupta* populations

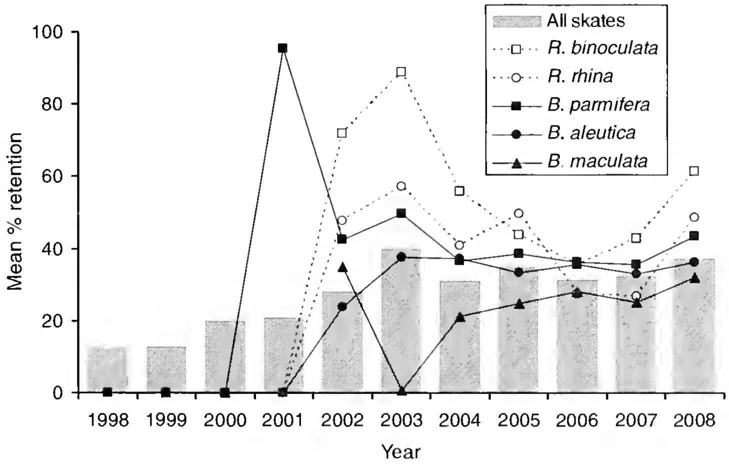

Figure 2

Overall mean percent retention of skate catch in commercial fisheries for each year from 1998 through 2008 (gray bars), as well as mean percent retention for *Raja binoculata*, *R. rhina*, *Bathyraja parmifera*, *B. aleutica*, and *B. maculata*.

are concentrated (Hoff and Britt, 2003, 2005, 2009; Stevenson et al., 2008).

In the Aleutian Islands, over 50% of OSC consists of *B. parmifera*, *B. maculata*, and *B. aleutica* (Table 2), which are the top three species in terms of recent biomass estimates for the region (Zenger, 2004; Rooper, 2008; Rooper and Wilkins, 2008). However, the proportion of *B. parmifera* is higher (29.6% of observed skate catch) and that of *B. maculata* considerably lower (12.1%) in commercial catches in the Aleutian Islands than their biomass estimates in the region (20–25% and 48% of total skate biomass, respectively) would indicate. The reasons for these differences in relative catch weight are unclear, but may be due to geographically and bathymetrically concentrated commercial fishing effort. Skate populations in Alaska are primarily segregated by depth, and *B. maculata* tends to be found in deeper waters than those inhabited by *B. parmifera* (Rooper, 2008; Stevenson et al., 2008). Therefore, shallow-water fisheries are more likely to catch *B. parmifera*, and although observers reported skates in the Aleutian Islands from depths to 2000 m, the majority of OSC came from 200 m or less. Thus, Aleutian populations of *B. parmifera* may be disproportionately affected by fishing activity because of the shallow depth distribution of this species.

The two species of *Raja* (and unidentified *Raja*—"*Raja* sp.") account for over 60% of OSC in the Gulf of Alaska. These results are also consistent with fishery-independent survey data, which indicate that *Raja binoculata* and *R. rhina* are the most abundant species in the Gulf of Alaska, making up about 37% and 33%, respectively, of the skate biomass in the region (Stevenson et al., 2008; von Szalay et al., 2009). Among species of *Bathyraja* in the Gulf of Alaska, survey-derived biomass estimates indicate that *B. aleutica* is the most common, and indeed *B. aleutica* accounts for a greater proportion of OSC in this region than all other species of *Bathyraja* combined.

Deepwater skate species, such as *B. lindbergi*, *B. minispinosa*, and *B. trachura*, are rarely reported by observers in any of the three regions, probably due to the relatively small amount of fishing effort targeting deepwater species. Other species known to be rare in Alaska waters, such as *B. abyssicola*, *B. mariposa*, and *Amblyraja badia*, have been only rarely reported by observers, and only *B. mariposa* has been confirmed by photographs and collected specimens.

Although the percentage of unidentified skates in observer species composition data has declined to a very low level, a large percentage of OSC is still identified only to genus. These less specific skate identifications are largely the result of uncertainty with identification in the field. Because observers encounter a relatively high diversity of skates, particularly of the genus *Bathyraja*, and must often interpret subtle characteristics to identify skates to the species level, they are encouraged to identify a skate only to the genus level if the specimen is not brought to hand for inspection or if the identification of the specimen is questionable. As a result, species composition of OSC is clearly affected by fish-handling practices and observer sampling methods on vessels with different gear types. Observers in trawl fisheries select their species composition samples at random from the catch after it is onboard the vessel. Therefore, the entire composition sample is weighed, and all specimens in the composition sample are identified in hand. In contrast, on longline vessels species composition data are collected as the gear is being retrieved, and not all of the specimens in the composition sample are brought on board and weighed. Some specimens counted during the tally period, particularly larger species such as many of the skates common in Alaska waters, become "drop-offs." These specimens are retrieved to the surface on the line but either fall off before they can be brought onboard or are intentionally released to save strain on the gear, the personnel, and the fishes. Therefore, many of the skates in the composition sample from longline vessels are not brought to hand for identification, and are recorded at the genus level. Thus, the way the catch is handled and sampled in longline fisheries largely explain the influence of gear type on the species composition profiles reported here (Table 2).

The influence of longline data is significant because the majority of OSC in Alaska waters comes from longliners. In fact, the data presented here (Table 3) indicate that the longline fishery for Pacific cod in the Bering Sea accounts for more skate bycatch than all other federally managed groundfish fisheries combined. This result must be interpreted with some caution because differences in observer coverage for different fisheries and regions may have influenced these figures, and a predominant species is not a precise indicator of a target fishery. But it is clear that longliners targeting Pacific cod catch a lot of skates. Moreover, longline gear is often fished deeper than trawl gear, and therefore may affect a greater diversity of skate species than gear fished in more shallow water because skate diversity in Alaska waters tends to be highest on the continental slope (Stevenson et al., 2008). Therefore, as long as a high proportion of skates encountered on longliners are identified only to genus, a potentially important segment of species-specific catch data is still not available for analysis.

The presence of skates in the catch of pelagic trawls may seem counterintuitive because skates are generally benthic, substrate-oriented fishes unlikely to be found in the path of midwater nets. Indeed, the amount of skate catch reported in pelagic trawls (about 6% of OSC) is much lower than in the other two gear types. There are two general explanations for the skates that are collected in pelagic nets: either the skates were swimming up in the water column or the net contacted the seafloor. The target of most pelagic trawling in Alaska is walleye pollock, a species that is often found very close to the bottom, and catch data from pelagic trawlers often include a variety of benthic species, such as flatfishes and sculpins, in addition to skates. Therefore, it is likely that at least a large proportion of the skate

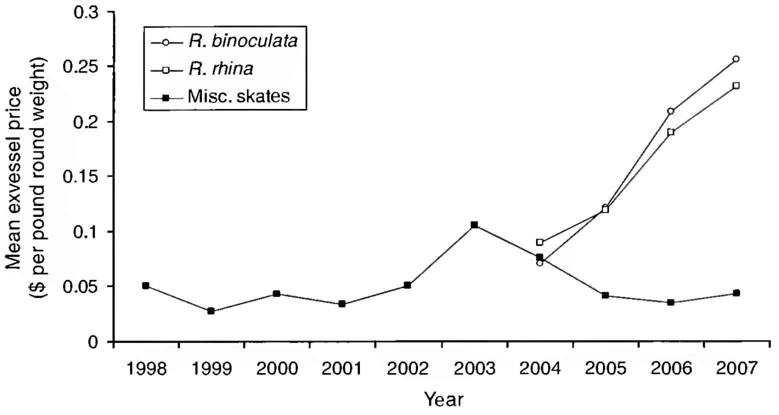

Figure 3

Annual mean exvessel price paid by processors in Alaska for big skate (*Raja binoculata*), longnose skate (*Raja rhina*), and miscellaneous skates from 1998 through 2007.

catch in pelagic trawls is the result of the net contacting, or at least coming very close to, the seafloor.

Historically, skates have not been considered valuable by Alaska's commercial fishermen. Even though skates are large fishes that represent a significant potential source of protein, retention of skates in the commercial fisheries of Alaska has been low. However, groundfish observer data, coupled with exvessel pricing information, may indicate that this situation is beginning to change. Overall mean retention was less than 15% in the late 1990s, and presumably before that time as well; however, it has increased to 30–35% in recent years. Species-level catch data collected since 2004 indicate that the large species (such as both species of *Raja*, *Bathyraja parmifera*, and *B. aleutica*) are retained at a higher rate than smaller species, and that retention rates for the large species are not necessarily consistent from year to year. The general increase in retention rates may reflect changes in the market value for skate products. Although the mean exvessel price for general skate catch has remained fairly stable over the past decade (Fig. 3), the price paid to Alaskan fishermen for big skates and longnose skates has risen sharply. Since 2004, when processors began reporting landings data by species owing to changes in the Fishery Management Plan for groundfish of the Gulf of Alaska, the mean annual price paid for big and longnose skates has nearly tripled.

Although the data presented here signify a dramatic improvement in the information available to fishery managers, some noteworthy gaps persist. The data presented here represent only sampled hauls on vessels requiring observer coverage in federally managed fisheries, and therefore other sources of skate bycatch are not represented. Commercial fishing activity in the Bering Sea and Aleutian Islands is conducted primarily on large vessels, which are required to have 100% observer coverage, and therefore observer data should provide a good representation of skate bycatch in those regions. In contrast, many of the commercial vessels operating in the Gulf of Alaska are small enough that observer coverage is only required on 30% of fishing days or is not required at all. Therefore, observer data for this region may provide much less reliable estimates of skate bycatch. Because the two species of the genus *Raja* are common in the Gulf of Alaska, and are among the largest skate species in the region, the unobserved catch of those species is of particular concern. Disproportionate retention of larger skates is prevalent in many fisheries worldwide, and as larger, more vulnerable species are removed, smaller species may become more abundant (Russ, 1991; Agnew et al., 2000; Cedrola et al., 2005; Swain et al., 2005). In the North Atlantic, severe reduction in biomass for some larger, less resilient skate species has been accompanied by an increased biomass for smaller, more resilient species (Casey and Myers, 1998; Walker and Hislop, 1998; Dulvy et al., 2000). Species-specific observer data on skate bycatch can document this phenomenon, but only if the data are representative of total fishing effort. Therefore, undocumented sources of skate bycatch, as well as nonspecific data from observed longline fisheries (see above comments on longline species composition data), present significant remaining challenges to fishery managers.

Observer data on skate bycatch in the groundfish fisheries of Alaska represent a rich source of information for managers charged with protecting skate populations from future overexploitation. The species-level catch data now being collected by observers have facilitated the development of an age-structured stock assessment model for *B. parmifera* (B. Matta, personal commun.[2]), which is a critical aid in setting appropriate catch limits for the species, and similar models for other species

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[2] Matta, Beth. 2009. NMFS Alaska Fisheries Science Center, Seattle, WA 98115.

are on the horizon. These fishery-dependent data can now be compared directly with fishery-independent survey data, creating two independent lines of evidence for management strategies. Specific catch data may also be used to identify areas in which the most vulnerable species may be most heavily impacted and thus can help identify areas in which restrictions or closures are necessary. Although observer data do not give a complete account of skate bycatch in the fisheries of Alaska, the information currently provided allows this diverse assemblage of species to be managed in a more biologically appropriate way than was possible in the past. As fishing pressure on Alaska's skate populations increases, the consequences of data deficiencies will be magnified, and observer data will play an increasingly important role in protecting skates from the declines in biomass and shifts in community structure that have befallen these fishes in other parts of the world.

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Effects of starvation on energy density of juvenile chum salmon (*Oncorhynchus keta*) captured in marine waters of Southeastern Alaska

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Abstract—We conducted laboratory starvation experiments on juvenile chum salmon (*Oncorhynchus keta*) captured in the neritic marine waters of northern Southeast Alaska in June and July 2003. Temporal changes in fish energy density (whole body energy content [WBEC], cal/g dry weight), percent moisture content, wet weight (g), length (mm), and size-related condition residuals were measured in the laboratory and were then compared to long-term field data. Laboratory water temperatures and salinities averaged 9°C and 32 psu in both months. Trends in response variables were similar for both experimental groups, although sampling intervals were limited in July because fewer fish were available (n=54) than in June (n=101). Overall, for June (45-d experimental period, 9 intervals), WBEC, wet weight, and condition residuals decreased and percent moisture content increased, whereas fork length did not change. For July (20-d experimental period, 5 intervals), WBEC and condition residuals decreased, percent moisture content and fork length increased, and wet weight did not change. WBEC, percent moisture content, and condition residuals fell outside the norm of long-term data ranges within 10–15 days of starvation, and may be more useful than fork length and wet weight for detecting fish condition responses to suboptimal environments.

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Energy density is an important measure of fish nutritional condition and is used to assess growth, construct energy budgets, and measure energy flow in ecosystems (Brett et al., 1969; Jobling, 1994; Ban et al., 1996; Edsall et al., 1999). Energy density is also a critical parameter for bioenergetic models (Orsi et al., 2004; Trudel et al., 2005; Wuenschel et al., 2006; Breck, 2008). Along with other measures of fish condition, such as body composition, growth, and length-weight condition indices, energy density integrates and reflects the history of fish feeding environments before the time of sampling (LeBrasseur, 1969; Edsall et al., 1999; Breck, 2008). During good feeding periods, fish condition will be high, whereas the reverse is expected during poor feeding periods as energy reserves are depleted to maintain standard metabolic needs (Jobling, 1994). However, an examination of how quickly energy density responds during periods of poor feeding that are usually associated with low growth has been limited to a few studies. In general, a balanced energy budget is expressed as the equation: *ingestion* = *metabolism* + *growth* + *excretion*, which outlines how an energy source is used by an organism and what proportion is allocated to each component of the equation (Jobling, 1994; Brett, 1995). These allocations depend on the initial amount of energy, as well as the environmental conditions that affect physiological rates, such as temperature and salinity (Brett et al., 1969; Hoar, 1988; Jobling, 1994). When fish are starved, growth typically ceases and energy density declines; when energy stores are used, the percentages of fat and protein in the fish decrease as the relative water content increases (Brett, 1995; Breck, 2008). Changes in fish energy density may be more detectable on small scales than other fish parameters, such as growth, during periods of poor feeding conditions in marginal habitats.

Juvenile Pacific salmon (*Oncorhynchus* spp.) use transitional habitats along their seaward migration from near shore to the open ocean and can experience rapid environmental changes that may affect growth and energy allocation (Orsi et al., 2000; Cross et al., 2008). Fish transit these demanding environments at the same time that they are experiencing increasing energy demands while undergoing ontogenetic changes in metabolic rate related to salinity and smoltification (Hoar, 1998). These transitional habitats are presumed to be critical feeding areas because prey fields also change dramatically, and juvenile salmon are often found in the presence of planktivorous forage fish species that potentially impact carrying capacity (Purcell and Sturdevant, 2001; Park et al., 2004; Orsi et al., 2004). Therefore, understanding how changes in juvenile salmon energy density reflect habitat quality may give insight into factors that affect their growth and survival, particularly if food resources may be limited during this critical time in their life history (Paul and Willette, 1997; Boldt and Haldorson, 2004; Cross et al., 2008).

We initiated a study to measure changes in condition of juvenile chum salmon (*O. keta*) captured at sea and later denied food resources in the laboratory. In previous studies on fish starvation, juvenile chum salmon were reared entirely in the laboratory (LeBrasseur, 1969; Akiyama and Nose, 1980; Murai et al., 1983; Ban et al., 1996); however, in our study they experienced variable environmental conditions at sea before being captured and transported back to the laboratory. Thus, these salmon from field collections represent natural variation of fish in marine waters better than fish reared in controlled laboratory environments. Our primary objective was to measure changes in energy density, moisture content, weight, length, and a size-related condition residual index for field-caught juvenile chum salmon in response to starvation in the laboratory over time. We also compared the condition of these experimentally starved fish to that determined from a long-term data series on field-caught fish 1) to assess the range of normally occurring condition values and 2) to identify the length of time before experimental values fell outside the observed range.

Methods

Juvenile chum salmon for the experiments were captured in the vicinity of Icy Strait (58°N latitude, 135°W longitude) about 50 km west of Juneau, Alaska, in June and July 2003. Fish were obtained during the Southeast Alaska Coastal Monitoring (SECM) Project long-term annual survey of juvenile salmon by the Auke Bay Laboratories (ABL) aboard the NOAA ship *John N. Cobb* (Orsi et al., 2004). Juvenile chum salmon were collected from the neritic waters of Icy Strait and Upper Chatham Strait, along the primary seaward migration corridor in the northern region of Southeast Alaska (Orsi et al., 2000, 2004). Preliminary observations along this corridor showed that juvenile chum salmon exhibit approximately a five-fold increase in body length, 100-fold increase in weight, 25% increase in energy density, and more than 6% decline in body moisture content between May and September. We used fish from this locality in June and July, the periods of highest abundance and greatest interaction with other juvenile salmon species. In June, fish were captured with a Kodiak pair-trawl fished at 1 m/sec for 10 min (Mortensen et al., 2000). In July, fish were captured with a Nordic 264 rope trawl fished at 1.5 m/sec for 20 min (Orsi et al., 2000). All fish caught were immediately transferred from the trawl codend to static live tanks containing sea water. Juvenile chum salmon were then identified and sorted into flow-through "live" tanks. The sea water for the tanks was pumped from a depth of 3 m and then filtered to prevent feeding on zooplankton prey. Before transfer to the laboratory, the juvenile chum salmon were held onboard for one day in June and four days in July while the surveys were completed. To establish a baseline for the start of the starvation experiments, on the day of capture a subsample of fish were measured (fork length, FL, mm) and frozen (−5°C) for later laboratory analysis. Daily temperature and salinity measurements were recorded and averaged 11.4°C and 26.1 psu in June and 12.7°C and 23.2 psu in July.

In the laboratory, the juvenile chum salmon were placed in two living-stream tanks (Frigid Units, Inc., Toledo, OH) (200×50×48 cm) with screened baffles separating the inflow and outflow pipes. One unit was allocated the salmon captured in June; the other unit—the salmon captured in July. Ambient sea water from a 25-m depth in Auke Bay was supplied to the tanks at a rate of 3 L/min. Daily temperature and salinity measurements were recorded in the laboratory tanks and averaged 8.6°C and 31.7 psu for June and 8.6°C and 32.1 psu for July. Sea water was filtered to prevent feeding on zooplankton prey. The fish were not subjected to any strong currents that would increase activity costs. To best mimic the photoperiod in the natural environment at the time of capture, light conditions in the laboratory were set at a standard eight hours of darkness, one hour of dusk, one hour of dawn, and 14 hours of daylight. Subsamples of 10–15 fish were removed from the tank at predetermined intervals and sacrificed with an overdose of tricaine methanesulfonate (MS-222), then frozen (−5°C) individually for later size and calorimetric analyses. Fish that had died between sacrifice intervals were not included in the experiments.

Frozen juvenile chum salmon were processed for data, including energy density in terms of whole body energy content (WBEC, cal/g wet weight [WW]), dry weight (DW, mg), percent moisture content (%MC), FL, and wet weight (mg). After excising each stomach and removing and weighing its contents, we dried the fish to obtain DW (full gut minus empty gut, nearest mg) so that undigested prey would not bias the final values. Stomachs examined from fish sacrificed after the first time interval were devoid of prey and therefore stomachs were not excised in subsequent time intervals. All viscera were replaced in the body cavity before the fish were dried to a stable weight (≤5 mg change), requiring a minimum of 48 hours at 55°C. The DW was recorded and %MC of each fish was calculated as ($[1-DW/WW] \times 100$). Each fish was homogenized with a Waring pulverizer, then finely ground with a mortar and pestle to yield a uniform powder. Susamples of 15 mg were formed into pellets with a pellet press and stored in a desiccator to prevent rehydration. A 1425 Parr micro-bomb calorimeter was used to obtain cal/g DW for each fish; this measure was converted to WBEC by multiplying by DW/WW. Estimates of WBEC from replicate subsamples were consistent (<2% coefficient of variation). To account for potential effects of size variation on WBEC and %MC, size-related condition residuals (CR) were calculated by using the ln-transformed experimental FL and WW measures for each fish. We first derived a regression equation from all paired ln-weights and ln-lengths (n=8475; ~700 per year) of field-caught juvenile chum salmon collected during June–August for the SECM project from 1997 to 2008. We then used this regression equation to predict ln(WW) for each experimental ln(FL). Finally, we obtained the CRs by subtracting the predicted ln(WW) from the observed ln(WW) (Jakob et al., 1996; Brodeur et al., 2004).

To account for potential stock-related differences in condition of the experimental chum salmon (of unknown stocks), WBEC was determined for additional field-caught fish of known stocks. Historically, between 70% and 90% of fish caught in June originated from Macaulay Hatchery (MH), whereas mixed hatchery stocks were present during July (Orsi et al., 2004). Otoliths were not retained from the fish used in the experimental groups; however, stock of origin was determined from thermal marks present on the otoliths of juvenile chum salmon captured in the study area in July and these marks indicated that the fish were from unmarked stocks (UM, presumably wild) and MH and Hidden Falls Hatchery (HF) stocks. Both hatcheries mark 100% of chum salmon released. Energy densities were determined (as described above) for these three stock groups.

One-way analyses of variance (ANOVA) were used for initial statistical analyses to compare WBEC, %MC, FL, and WW of fish across sampling intervals for each experimental group and for July stock groups. If significant differences were detected, Tukey's paired comparison tests were performed to identify the interval in which they were found. We used graphical analyses to compare the WBEC and %MC for each experimental group to the norms (one standard deviation about the mean) derived from the entire SECM field data set (1997–2008) from June and July (n=1257; WBEC: 993.4 ±72.3 and %MC: 79.4 ±1.2). The temporal data from the experiments were compared to these norms to identify the duration of starvation before the experimental measures fell outside the long-term range of field values.

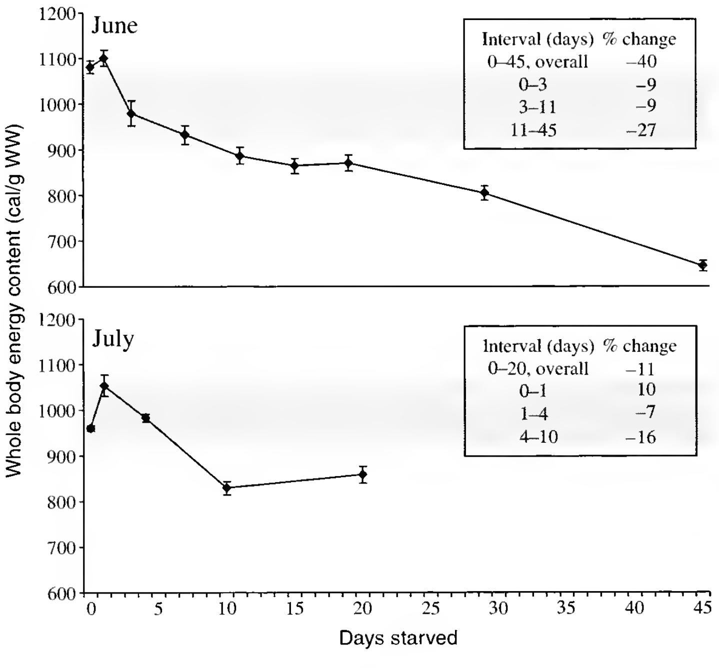

Figure 1

Average whole-body energy content (WBEC, cal/g wet weight) and one standard error about the mean for juvenile chum salmon (*Oncorhynchus keta*) starved over time in the laboratory after capture in the marine waters of Icy Strait and Upper Chatham Strait in the northern region of southeastern Alaska, June and July 2003. The grey band indicates one standard deviation about the mean for all field-caught juvenile chum salmon examined for WBEC during the Southeast Coastal Monitoring project, June–July (n=1257), 1997–2008. Significant differences (Tukey's paired comparisons; P<0.05) and percent change between sample intervals are shown in inset boxes.

Results

The numbers of juvenile chum salmon obtained for the two starvation trials included 101 fish for June and 54 fish for July. The higher number of juvenile chum salmon available in June allowed nine experimental time intervals to be tested, spanning 45 days (mean of five days per interval, range of 1–16 days between intervals). The smaller number of juvenile chum salmon available in July allowed only five experimental time intervals to be tested, spanning 20 days (mean of five days per interval, range of 1–10 days between intervals). Both experimental groups had common intervals at about 10 and 20 days. Mortality between sampling intervals was minimal in both groups: 13 fish died in June (70% during the first 10 days of the experiment) and two died in July (both during the first 2 days).

The energy content of juvenile chum salmon declined over time in both experimental groups (Fig. 1). Initial WBEC was significantly higher in June than in July (1081.2 cal/g WW compared to 960.5 cal/g WW; P<0.001). For the June sample group, WBEC decreased significantly (P<0.001) by 19% between days zero and 19 and by 40% between days zero and 45; see table insets in figures for significant differences (Tukey's paired comparisons) between intervals. For the July sample group, WBEC decreased significantly (P<0.001) by 11% between days zero and 20. Overall, the relative loss of energy content was almost twice as great in June as in July at day 20.

In contrast to WBEC, %MC of juvenile chum salmon increased over time in both

Table 1

Average fork length (FL, mm), wet weight (WW, g), percent moisture content (%MC, [(1–*dry weight*/*WW*)×100]), and whole body energy content (WBEC, cal/g WW), for unmarked (presumably wild) and hatchery stock groups of juvenile chum salmon (*Oncorhynchus keta*) captured in the marine waters of Icy Strait and Upper Chatham Strait in the northern region of southeastern Alaska, July 2003. Standard errors are given in parentheses.

Stock group	*n*	FL	WW	%MC	WBEC
Unmarked	13	120 (1.7)	17.5 (0.8)	80.4 (0.1)	954.0 (5.7)
Macaulay Hatchery	10	137 (3.0)	29.0 (1.5)	80.3 (0.2)	957.5 (14.3)
Hidden Falls Hatchery	10	127 (2.9)	22.1 (1.6)	80.4 (0.1)	959.5 (9.6)

experimental groups (Fig. 2). Initial %MC was significantly lower ($P<0.001$) in June than in July (77.8% compared to 80.1%). For the June sample group, %MC increased significantly ($P<0.001$) by 4% between days zero and 19 and by 9% between days zero and 45. For the July sample group, %MC increased significantly ($P<0.001$) by 1% between days zero and 20. Overall, the increase in %MC was four times as great in June as in July at day 20.

Changes in the WW and FL of juvenile chum salmon over time were not consistent between the experimental groups (Fig. 3). For WW, initial values did not differ ($P>0.05$) between June and July (14.2 compared to 13.6 g). For the June sample group, WW decreased significantly ($P<0.01$) by 39% between days zero and 45. For the July sample group, no significant ($P>0.05$) differences in WW were observed. Similarly, initial FL values did not differ ($P>0.05$) between June and July (112 compared to 110 mm). For the June sample group, FL did not change significantly ($P>0.05$) between days zero and 45. For the July sample group, FL increased significantly ($P<0.001$) by 19% between days zero and 20.

The CR of juvenile chum salmon became increasingly negative over time in both experimental groups (Fig. 4). Initial CRs were positive in both months, but June CRs were lower than those for July. For the June sample group, CR declined significantly ($P<0.001$) between days zero and 19 and between days zero and 45. For the July sample group, CR declined significantly ($P<0.001$) between days zero and 20. Mean CRs shifted from positive to negative after approximately 10 days of starvation in each sample group and continued to decline, indicating increasingly poor condition for a given size fish.

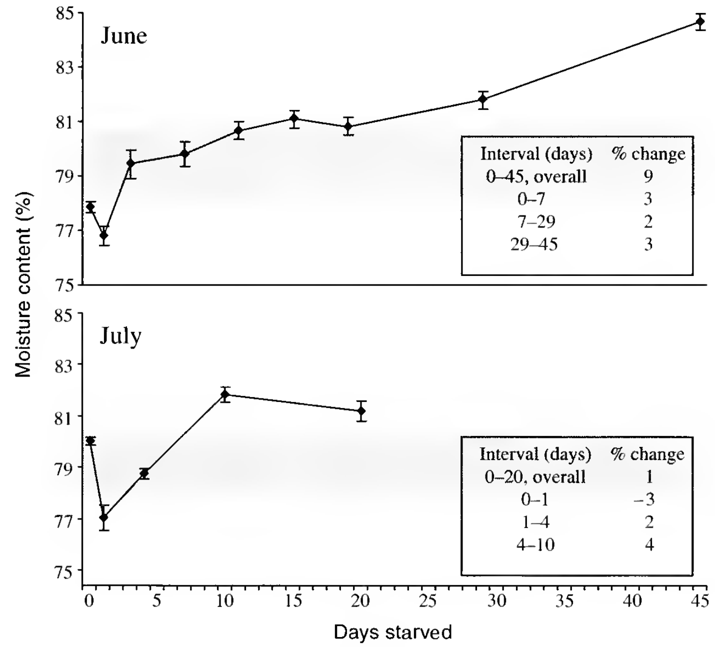

Figure 2

Average percent moisture content (%MC, [(1–*dry weight*/*wet weight*)×100]) and one standard error about the mean for juvenile chum salmon (*Oncorhynchus keta*) starved over time in the laboratory after capture in the marine waters of Icy Strait and Upper Chatham Strait in the northern region of southeastern Alaska, June and July 2003. The grey band indicates one standard deviation about the mean for all field-caught juvenile chum salmon examined for %MC during the Southeast Coastal Monitoring project, June–July (n=1257), 1997–2008. Significant differences (Tukey's paired comparisons; $P<0.05$) and percent change between sample intervals are shown in inset boxes.

Hatchery stock group did not affect the WBEC or %MC of the July-caught juvenile chum salmon. A total of 33 fish were examined: UM (n=13), MH (n=10), and HF (n=10) (Table 1). Stock had no effect on WBEC or %MC ($P>0.05$). However, WW and FL did differ significantly ($P<0.001$) among stocks and were highest for the MH stock and lowest for the UM stock (Table 1).

Discussion

To our knowledge, this is the first published study of the change in energy density and %MC of field-captured

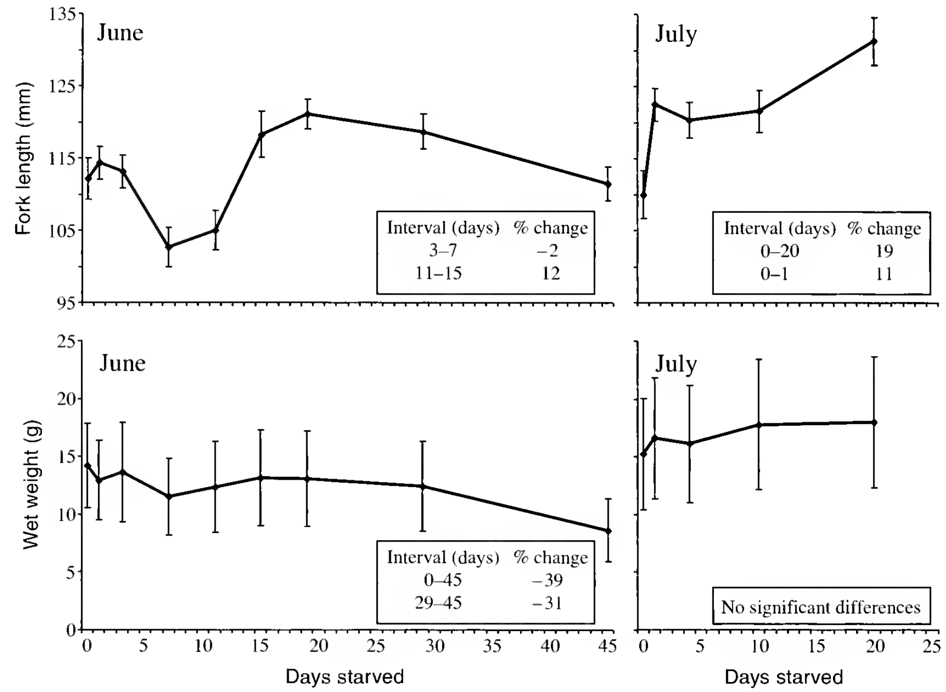

Figure 3

Average fork length (mm, top panels) and wet weight (g, bottom panels) for juvenile chum salmon (*Oncorhynchus keta*) starved over time in the laboratory after capture in the marine waters of Icy Strait and Upper Chatham Strait in the northern region of southeastern Alaska, during June (left panels) and July (right panels) 2003. Error bars are one standard error about the mean. Significant differences (Tukey's paired comparisons; $P<0.05$) and percent change between sample intervals are shown in inset boxes.

juvenile chum salmon during starvation. Limited information has been published on the changes in condition of laboratory-reared chum salmon due to starvation. Such studies typically show depletion of stored nutrients and declines in condition and size over time, despite differences in methods (LeBrasseur, 1969; Akiyama and Nose, 1980; Murai et al., 1983; Ban et al., 1996). For nutrient responses, lipid and serum protein levels of laboratory-reared juvenile chum salmon were lowest after 10 and 20 days of starvation, respectively (Ban et al., 1996); unfortunately, however, energy content was not determined. We did not directly measure lipid and protein, but the decline in WBEC that we observed between days zero and 10 and between days 20 and 45 in June could reflect similar declines in these nutrient measures. For condition responses, two studies showed that %MC of small starved juvenile chum salmon increased by 4.3% (41 mm and 0.45 g initial size; 42-d starvation; LeBrasseur, 1969) to 5.4% (0.26 g initial size; 28-d starvation; Murai et al., 1983) at ~15°C; another study showed that % MC of larger starved juvenile chum salmon increased by 12% (94.5 mm and 7.9 g initial size; 91-d starvation; Akiyama and Nose, 1980) at 17°C. Trends in %MC of our juvenile chum salmon were comparable despite the differences in fish size, duration of starvation, and water temperature. For size responses, weight decreased for five size-groups of juvenile chum salmon (0.46–7.95 g initial size; 5–13 wk starvation); however, the percentage weight loss decreased as fish size increased (Akiyama and Nose, 1980). These differences in weight loss among fish sizes indicate that physiological responses to starvation may vary with ontogeny.

Our results are also comparable to information available for other salmonid species and stages. For starved juvenile sockeye salmon (*O. nerka*), energy density declined more rapidly and %MC increased more rapidly with increasing temperatures (Brett et al., 1969). In our study, chum salmon in June exhibited a 40% decline in WBEC and a 9% increase in %MC after 45 days of starvation at an average temperature of ~9°C. By comparison, at similar temperatures (10°C), laboratory-reared juvenile sockeye salmon lost 37% of initial WBEC and gained 9% MC during 99 days of starvation (Table 3 in Brett et al., 1969). Such inverse relationships between fraction water and fraction lipid or energy content are often reported during starvation (Miglavs and Jobling, 1989; Simpkins et al., 2004; Breck, 2008). In a few studies, size changes similar to those that we observed have also been reported among other starved salmonids. Weight decreased for starved juvenile Arctic charr

(*Salvelinus alpinus*; Miglavs and Jobling, 1989), rainbow trout (*O. mykiss*; Simpkins et al., 2004), and Atlantic salmon (*Salmo salar*; Stefansson et al., 2009) for starvation periods of 4–6 weeks. Length and weight of small (30.1-mm and 0.14-g) sockeye salmon decreased significantly after 14–49 days of starvation in colder water (7.9°C; Bilton and Robins, 1973) than that used in our experiment. Like the salmonids in the above studies, weight of our juvenile chum salmon decreased for the June experimental group, but similar conclusions about the July fish could not be reported because of the shorter experimental period.

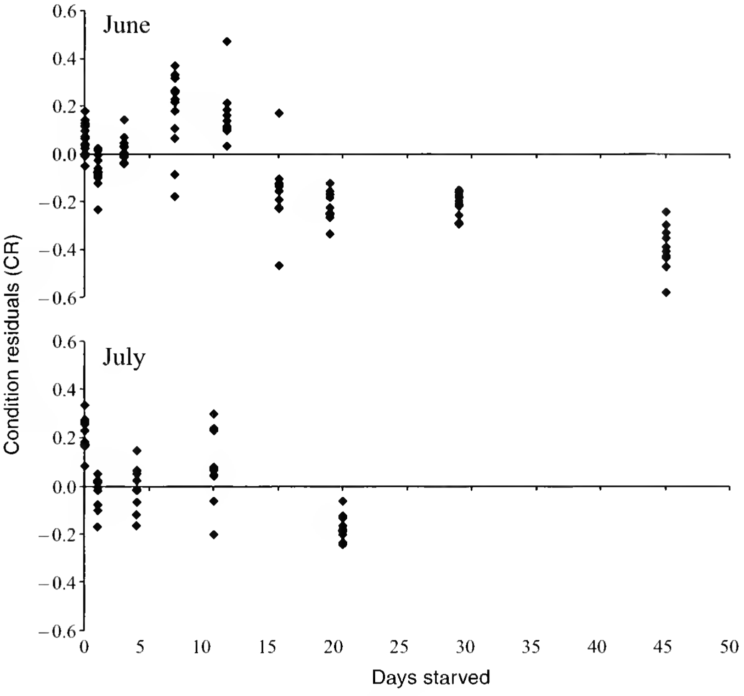

Figure 4

Condition residuals (CR) for individual juvenile chum salmon (*Oncorhynchus keta*) starved over time in the laboratory after capture in the marine waters of Icy Strait and Upper Chatham Strait in the northern region of southeastern Alaska, June and July 2003. The CRs were calculated by using the ln-transformed experimental fork length and wet weight measures for each fish in a regression equation derived from all paired ln-weights and ln-lengths of field-caught juvenile chum salmon collected during the Southeast Coastal Monitoring project, June–August (n=8476) from 1997 to 2008. The 0.0-line represents the expected CR of an average fish; therefore, positive values indicate above average condition and negative values indicate below average condition.

The chum salmon caught in June initially had approximately 11% higher WBEC and approximately 3% lower %MC than fish caught in July—differences that could be accounted for by both environmental and biological variables. In both the June and July experimental groups, a measurable increase in WBEC and decrease in %MC occurred between days zero and one. These changes may have been attributed to a physiological stress response that caused the fish to lose water and therefore increased the relative WBEC and decreased the %MC (Breck, 2008). Temperature and salinity both affect fish physiological rates and influence ingestion, metabolism, and growth (Brett et al., 1969; Mason, 1974; Sheridan et al., 1983; Jobling, 1994; Weatherley and Gill, 1995). In our study, field temperature was cooler and salinity was higher in June (11°C; 26 psu) than in July (13°C; 23 psu), but fish captured in both months were transferred into identical, colder (9°C) and more saline (32 psu) environments in the laboratory. Monthly differences in temperature and salinity were therefore eliminated as variables in the experiments. However, the fish captured in June had probably smolted more recently (Zaporozhec and Zaporozhec, 1993; Hoar, 1998) and spent less time in the marine environment, and probably had lower growth rates (Orsi et al., 2000) and energy requirements than fish captured in July, when it was warmer.

We accounted for potential size-related effects on WBEC and %MC by using length-weight regression analysis, which corrected for natural variation in fish size; however, the results may still be misleading because this regression did not account for differences in actual nutritional status or body composition, such as protein, lipid, and water content (Miglavs and Jobling, 1989; Edsall et al., 1999; Kotiaho, 1999; Trudel et al., 2005; Congleton and Wagner, 2006). Length-weight regression analysis is useful for initially identifying condition in relation to a long-term index and to anticipate trends in energy density, but to account for changes in nutritional status or body composition WBEC, %MC, or proximate composition, should be used to verify the CR results.

In our study, stocks of juvenile chum salmon sampled from the same habitat did not differ in WBEC or %MC, but size did differ significantly. By comparison, for juvenile pink salmon (*O. gorbuscha*) captured together in marine habitats of Prince William Sound, Alaska, differences in length and WBEC between stock groups have not been consistent (Paul and Willette, 1997; Boldt and Haldorson, 2004; Cross et al., 2008). For fish ~80 mm in length, the occurrence of length differences between juvenile pink salmon stocks depended on the size of hatchery fish at time of release (Cross et al., 2008). In a concurrent study, juvenile pink salmon length differed between stock groups, but WBEC did not (Boldt and Haldorson, 2004). Conversely, energy content (somatic) of smaller juvenile pink salmon (~35 mm) did differ between stock groups (Paul and Willette, 1997).

These studies, along with ours, support the idea that different stock groups of juvenile salmon may have similar WBEC in common habitats despite stock-specific size differences, and thus emphasize the importance of habitat quality on fish condition. These different results could also be related to ontogenetic changes in physiology (Hoar, 1998; Wuenschel et al., 2006).

Because so little mortality occurred within each experimental group, we conclude that juvenile salmon can survive for prolonged periods without food during the summer months, as has also been reported by Stefansson et al. (2009). Most of the mortalities occurred within the first eight days of the June experiment. As discussed previously, the June fish were younger and less robust (lower CR) and could have been more susceptible to environmental stresses because of scale loss (Bouck and Smith, 1979) from net abrasion during capture, for example. However, even though juvenile chum salmon were still alive after 45 days of starvation, many salmonids cannot recover physiologically after extended periods of starvation because of compromised seawater tolerance or impaired compensatory growth (Bilton and Robins, 1973; Ban et al., 1996; Stefansson et al., 2009); such recovery capabilities in juvenile chum salmon remain unclear.

The experimental WBEC, %MC, and CR differed from the long-term average of the SECM data sets during both months. After about 10 days of starvation, WBEC was below the normal range, %MC was above the normal range, and CR shifted from positive to negative, in both months. More specifically, by day 20, the June fish had lost twice their WBEC and CR, and had gained four times %MC as the July fish. The WBEC of the June fish required only 3–7 days of starvation before dropping to the lower initial level of the July fish.

Our study on the effects of starvation on field-caught juvenile chum salmon indicates that WBEC, %MC, and CR are more responsive measures than WW and FL to prolonged food deprivation in a controlled laboratory environment. Although starvation is an extreme case of limited food resources, clearly juvenile chum salmon can survive these conditions for extended periods, but may consequently be less tolerant of variable environmental conditions and more susceptible to other sources of mortality, such as predation. Future studies will focus on monitoring the seasonal response of juvenile salmon condition measures, such as WBEC, %MC, and CR, in different habitats at sea.

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Abstract—Determining the sex of thornyheads (*Sebastolobus alascanus* and *S. altivelis*) can be difficult under field conditions. We assessed our ability to correctly assign sex in the field by comparing results from field observations to results obtained in the laboratory through both macroscopic and microscopic examination of gonads. Sex of longspine thornyheads was more difficult to determine than that of shortspine thornyheads and correct determination of sex was significantly related to size. By restricting the minimum size of thornyheads to 18 cm for macroscopic determination of sex we reduced the number of fish with misidentified sex by approximately 65%.

Accuracy of sex determination for northeastern Pacific Ocean thornyheads (*Sebastolobus altivelis* and *S. alascanus*)

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Accurate sex-specific data are essential for fitting age-structured population dynamic models and estimating spawning biomass (Methot, 2000). Assessing sex ratio is of added importance if sex-based selectivity occurs within a fishery; because separate management measures may be required for male and female fish (Cochrane, 2009).

Thornyheads are a common continental slope species and support a large commercial fishery (Gunderson, 1997). Longspine thornyheads (*Sebastolobus altivelis*) are found from the Gulf of Alaska to southern Baja California, whereas shortspine thornyheads (*Sebastolobus alascanus*) are distributed from the Bering Sea to northern Baja (Orr et al., 2000). Longspine thornyheads generally inhabit depths greater than 400 m, have a distribution range to about 1400 m depth (Jacobson and Vetter, 1996), and a peak in abundance and spawning biomass at about 1000 m depth (Wakefield, 1990; Jacobson and Vetter, 1996). Shortspine thornyheads are found from 20 m to over 1500 m in depth, are most abundant in the range of 180 to 450 m, and the majority of the spawning biomass occurs between 600 and 1400 m, where longspine thornyheads are most abundant (Jacobson and Vetter, 1996). The maximum size of shortspine thornyheads (>70 cm) is larger than that of longspine thornyheads (~38 cm). Shortspine thornyheads migrate to deeper water as their body size increases, whereas longspine thornyheads do not migrate to deeper water with increasing size.

Identifying the sex of mature longspine thornyheads and shortspine thornyheads by gross visual examination is difficult when gonads regress to a resting state (Pearson and Gunderson, 2003) because male and female gonads are small, not fully developed, and are morphologically similar. Determining the sex of individual thornyheads collected during the annual Northwest Fisheries Science Center (NWFSC) West Coast Groundfish Bottom Trawl Survey is difficult because the survey occurs from May to October when thornyheads are not reproductively active and gonads are in a resting state (Moser, 1974; Wakefield, 1990).

The addition of sex identification for both thornyhead species to survey sampling protocols will improve the information available for management of the resource. To address concerns about the ability of field personnel to correctly determine sex of thornyheads while at sea, we examined the sex of longspine and shortspine thornyheads in the laboratory using macroscopic examination of gonads (as a correlate for field work) in contrast to microscopic techniques (for confirmation of results). An additional goal was to determine a minimum size below which the error rate for classification of sex of thornyheads in the field was judged to be too high by investigating the relationship between sex misidentification and length, geographic area, and month captured. Because assessment scientists are interested in the actual proportion of males to females, we also evaluated absolute percent error after accounting for the portion of the error that was cancelled out by balancing the number of misidentified males reported as females against the number of misidentified females reported as males.

Materials and methods

The 2003 NWFSC West Coast Groundfish Bottom Trawl Survey was conducted between 24 June and 23 October, from the area off Cape Flattery, Washington (48°10'N lat.) to the U.S.-Mexico border (32°30'N lat.) at water depths of 55–1280 m. The survey area was covered twice by chartered commercial fishing vessels (20 to 28 m length). The first sampling period was from 24 June to 13 August and the second from 31 August to 23 October. A stratified random sampling design was used and the survey area was subdivided into adjacent cells of equal area (1.5 nmi long. by 2.0 nmi lat., Albers equal area projection). A total of 620 primary sites were randomly selected from cells stratified by geographic location and depth. The geographic allocation was based on assigning 15–25% of the cells to each of five International North Pacific Fisheries Commission (INPFC) statistical areas: U.S.-Vancouver (47°30'N to U.S.-Canada border), Columbia (43°00' to 47°30'N), Eureka (40°30' to 43°00'N), Monterey (36°00' to 40°30'N), and Conception (U.S.-Mexico border to 36°00'N). The survey area was further stratified into depth zones with 45% of the cells allocated to the shallow depth zone (55–183 m), 30% to mid-depth (184–549 m) and 25% to the deep stratum (550–1280 m). Each of four chartered fishing vessels was assigned 155 stations to sample.

The bottom trawl survey is a standardized fishery independent survey and all fishing operations are conducted in strict compliance to national protocols (Stauffer, 2004). Vessels were equipped with standard Aberdeen-style nets with small mesh (1.5-inch stretched measure) liner in the codend. All thornyheads randomly selected for biological sampling were assigned a unique identification number, individually weighed (kg), measured (fork length, cm), and frozen while at sea. All frozen specimens were brought back to the laboratory where fish were thawed, dissected, and examined macroscopically to identify sex. For macroscopic examination of gonads, an incision was made with a scalpel on the ventral surface of each thornyhead from the vent to the base of the pectoral fin. The lateral side of the fish was opened to expose the gonads, and a visual identification of sex was based on the physical structure of the gonadal tissue as described by Lagler et al. (1962). Sex was recorded as male, female, or unknown. For microscopic identification of sex, a section of gonad tissue from each fish was placed on a glass microscope slide, stained with acetocarmine solution and compressed with a cover slip. The stain acted on the gonad tissue by readily staining oocytes dark pink (Guerrero, 1974). The slides were viewed under a 10× power microscope (Leica DM LS2, Bannockburn, IL), and females were distinguished from males by the presence of dark pink stained oocytes.

Accuracy of sex determination was examined in relation to length by species, geographic region, and month of capture (June–October). To determine a size threshold below which sex determination should not be attempted in the field, we examined both the total and absolute percentage of incorrectly sexed thornyheads in relation to length. To avoid biasing results, we did not consider our ability to correctly identify female thornyheads at smaller sizes, as opposed to our ability to correctly identify males at smaller sizes. Absolute error was calculated as the absolute value of misidentified males minus misidentified females divided by the total number examined at each 1-cm size interval, and this value was then expressed as a percentage. Size data were transformed (natural logarithm) to reduce heterogeneity of variance before statistical analysis. Data were statistically compared by analysis of variance (ANOVA) by using SAS for Windows (SAS Institute, Inc., Cary, NC). Significant ANOVAs were followed by a nonparametric comparison of means test (Tukey's test). Fish in which the gonad could not be found, stained, or microscopically identified were not included in the analyses.

Results

A total of 574 successful tows were completed. Figure 1 shows the distribution and relative abundance (kg/ha) of thornyheads from the 2003 survey. Both species were concentrated in the mid- and deep depth strata (183–1280 m) and exhibited higher relative abundance north of Pt. Conception, CA (34°30'N lat.). Longspine thornyheads were collected in 214 tows at depths of 328–1280 m (mean depth 802 m) and shortspine thornyheads were collected in 311 tows at depths of 88–1280 m (mean depth 605 m). A total of 2325 thornyheads were collected for later processing in the laboratory. Sex was determined for 852 longspine thornyheads and 1148 shortspine thornyheads. Sex was indeterminable for 189 longspine and 136 shortspine thornyheads (average

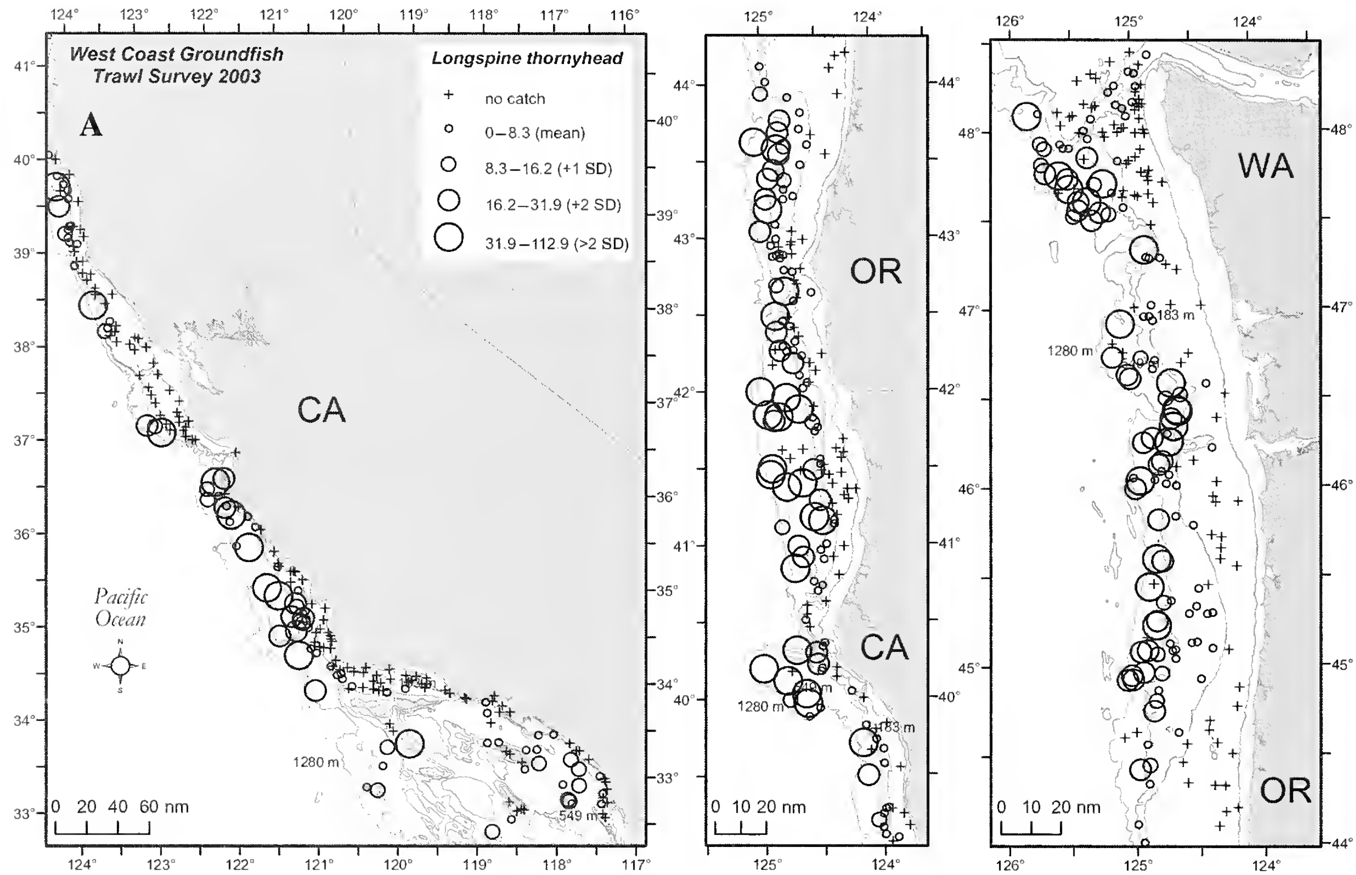

Figure 1

Distribution and relative abundance (kg/ha) of (**A**) longspine thornyhead (*Sebastolobus altivelis*) and (**B**) shortspine thornyhead (*Sebastolobus alascanus*) determined from the 2003 Northwest Fisheries Science Center west coast groundfish trawl survey. SD=standard deviation.

length 14.3 cm). Longspine thornyhead sex was misidentified by visual examination in 23.1% of males and 22.4% of females, and for shortspine thornyheads, in 9.4% of males and 9.3% of females.

Average lengths of longspine and shortspine thornyheads (females, males, and total) for which sex was misidentified were significantly lower than the lengths for fish whose sex was correctly assigned (Table 1). For shortspine thornyheads, the average length of sex-misidentified females was significantly smaller than that of males (ANOVA: df=6, F=5.5, P=0.02). Similar tendencies were seen for longspine thornyhead lengths but the results were not significant (Table 1).

Determining sex for longspine thornyheads greater than 22 cm would eliminate approximately 80% of the overall error rate, but would also eliminate 50% of the fish whose sex was correctly determined. By proposing 18 cm as the minimum size for examining longspine thornyheads in the field we eliminated approximately 65% of the incorrectly sexed fish, while retaining >70% of those correctly sexed (Fig. 2A). On average, the sex of 50.5% of longspine thornyheads ranging in size from 11 to 17 cm was incorrectly determined. This average dropped to approximately 10% for longspine thornyheads at lengths from 18 to 34 cm. A similar result was seen for shortspine thornyheads (Fig. 2A). The average percentage of shortspine thornyheads with misidentified sex was 53.7% at lengths from 11 to 17 cm. This value decreased to 5.9% for larger fish (18–71 cm) (Fig. 2A).

With a single exception, more males were misidentified as females in every size category for both species, and the absolute percentage of sex-misidentified fish decreased at fork lengths greater than 17 cm (Fig. 2B). For longspine thornyheads the average decreased from 15.8% for fish 11–17 cm to 2.2% for fish 18–34 cm length and the average percentage for shortspine thornyheads dropped from 24.5% to 3.0% in the larger size category (Fig. 2B).

Sex misidentification in longspine thornyheads did not vary significantly by month from June through October (ANOVA: df=7, F=1.74, P=0.34; Fig. 3A). However, sex misidentification for shortspine thornyheads was significantly higher in August, with an increasing trend from June through August followed by a decline (ANOVA: df=7, F=15.5, P=0.02; Fig. 3A).

The accuracy of sex determination varied by geographic area for both species (Fig. 3B). The sex of longspine thornyheads was more frequently misidentified

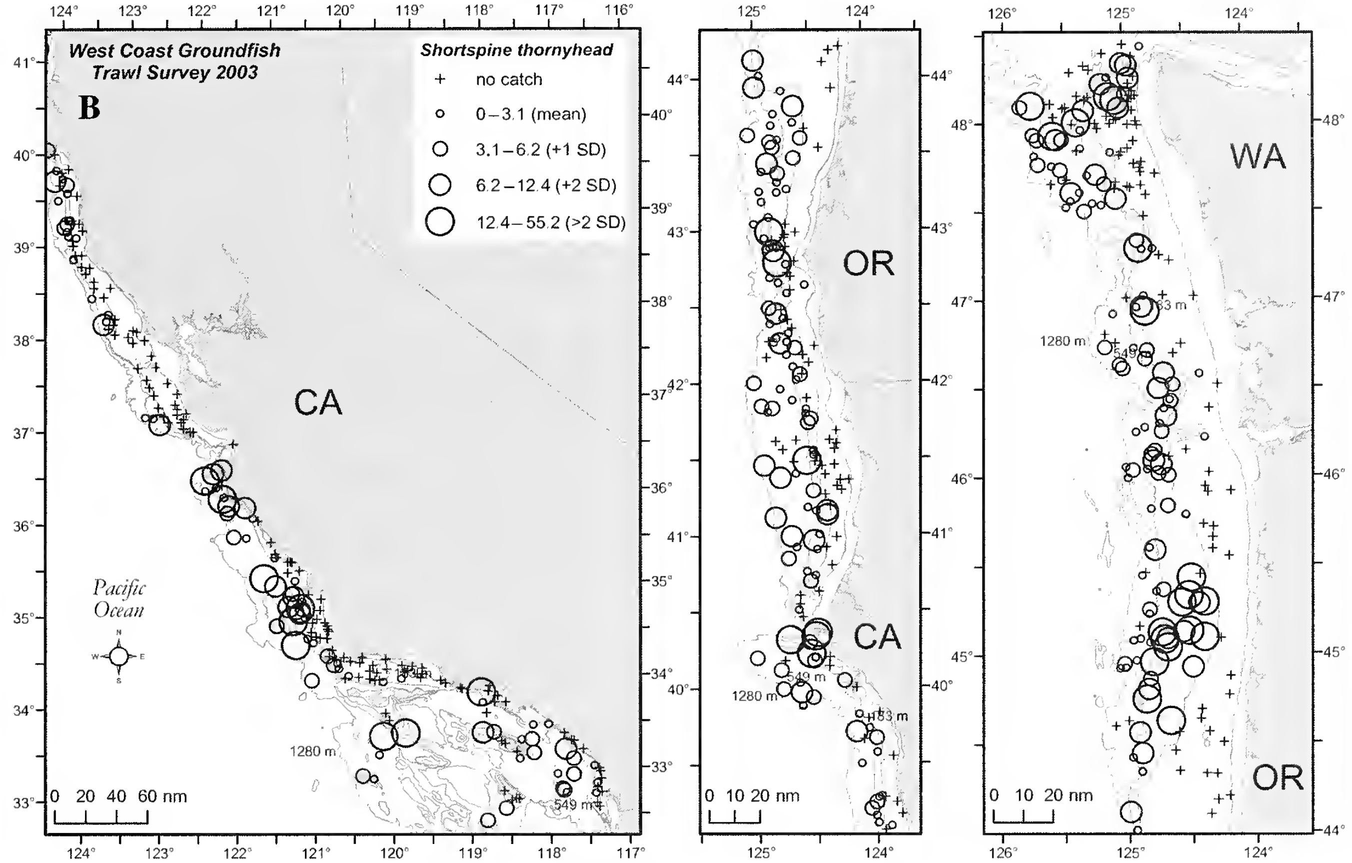

Figure 1 (continued)

Table 1

Number (n), mean fork length (cm, ±standard error [SE]), and analyses of variance (ANOVAs) for sizes for female, male, and total longspine (*Sebastolobus altivelis*) and for female, male, and total shortspine thornyheads (*S. alascanus*) captured during the 2003 Northwest Fisheries Science Center west coast groundfish trawl survey, correctly and incorrectly assigned sex based on visual examination.

	Correct		Incorrect		ANOVAs		
Species	n	Mean length (±SE)	n	Mean length (±SE)	df	F	P
Longspine thornyhead							
female	396	21.6 (0.21)	114	18.5 (0.37)	509	48.9	0.0001
male	259	23.4 (0.20)	83	19.0 (0.47)	341	96.6	0.0001
total	655	22.3 (0.15)	197	18.7 (0.29)	851	52.7	0.0001
Shortspine thornyhead							
female	560	35.5 (0.52)	58	23.6 (1.16)	617	50.8	0.0001
male	481	34.9 (0.45)	49	28.1 (1.52)	529	21.5	0.0001
total	1041	35.2 (0.35)	107	25.7 (0.96)	1147	36.2	0.0001

above 43°N latitude, and the U.S.-Vancouver and Columbia areas had a significantly higher average percentage of misidentification than the Eureka, Monterey, and Conception areas (ANOVA: df=4, F=44.1, P=0.007). The sex of shortspine thornyheads became more difficult to correctly identify below 40°N latitude, and both the Monterey and Conception areas had a significantly higher average percentage of misidentification compared to the Eureka, Columbia, and U.S.-Vancouver areas (ANOVA: df=4, F=13.9, P=0.03). There were no

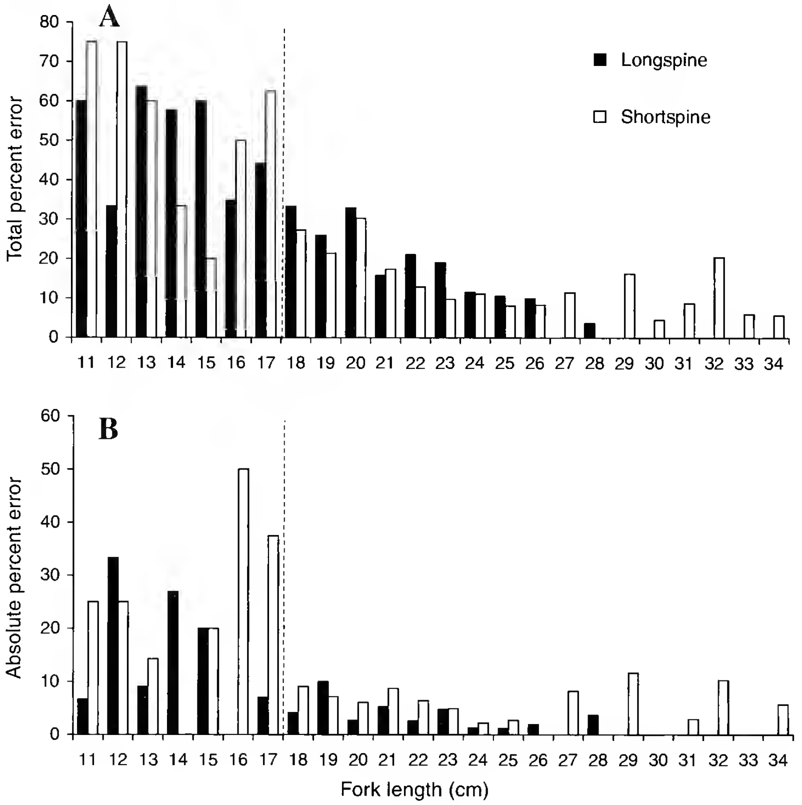

Figure 2

(**A**) Total percentage of sex-misidentified longspine (*Sebastolobus altivelis*) and shortspine thornyheads (*Sebastolobus alascanus*) determined by comparing the gross morphological features of gonads to a section of each gonad subsequently stained and viewed microscopically, by size (fork length, cm); and (**B**) the absolute percent error in identifying the sex of thornyheads after accounting for the portion of the total error that is cancelled out by balancing the number of sex-misidentified males against the number of sex-misidentified females.

significant differences in mean fork length for longspine thornyheads between the different areas (ANOVA: df=858, F=0.3, P=0.9), but for shortspine thornyheads, size was significantly larger in the Monterey and U.S.-Vancouver areas (ANOVA: df=1140, F=4.7, P=0.0009), and large fish in the Monterey area had a higher rate of individuals for which sex was incorrectly determined than similar size shortspine thornyheads in the U.S.-Vancouver area.

Discussion

This study provides guidance for a minimum size limit below which sex of thornyheads should not be determined at-sea because of high error rates. High quality biological information is important for management and modeling of thornyhead populations along the U.S. west coast (Fay, 2005). Fishery scientists need estimates of sex ratio for fish populations because shifts in these values can indicate overfishing on one sex or the other due to selective gear, differential growth rates, segregation by sex or any combination of these (Cochrane, 2009).

In previous studies of the reproductive biology of thornyheads, the longspine thornyhead spawning was determined to begin in January, peak in February and March, and continue at least through April (Wakefield, 1990; Pearson and Gunderson, 2003; Cooper et al., 2005). Shortspine thornyheads spawn between December and May along the U.S. west coast. The onset of sexual maturity occurs at 17–19 cm total length (10% mature females) in both species and 90% are mature at 25–27 cm (Pearson and Gunderson, 2003). Sex of smaller thornyheads is difficult to determine, particularly during the summer, because of the small size of the gonads—size being a function of the annual spawning cycle. Pearson and Gunderson (2003) noted that of 36 longspine thornyheads designated as immature females in the field on the basis of gross morphological features, nine were actually males.

Correct visual identification of sex for both shortspine and longspine thornyheads increased in fish longer than 17 cm. Overall accuracy is greater for shortspine than for longspine thornyheads, and greater for females than for males, and this accuracy is related to size in both instances. For both species, 18 cm was selected as the lower limit for determining the sex of thornyheads in the field because the majority of sex-misidentified fish fell below this value. In 2003, 66% of the longspine thornyheads and 90% of the shortspine thornyheads measured in the field throughout the survey period were greater than 17 cm. The selected size falls within the range of lengths noted for the onset of sexual maturity in both species.

Because the survey is conducted after the completion of the spawning season for longspine thornyheads (January–April), the samples are collected exclusively during the reproductive resting stage. Sex misidentification was relatively constant for longspine thornyheads throughout the sample period and there were no significant differences among months. Sex misidentification was greater for longspine than for shortspine thornyheads for each time period. The lower rate of sex misidentification for shortspine thornyheads may be related to their longer spawning season (December–May). Differences in the reproductive cycles of the two species resulted in the cessation of spawning coinciding with the start of the survey sampling for shortspine thornyheads and may partially explain the observed overall lower rate of sex misidentification for this species. The middle of the reproductive resting-stage period correlated with high levels of sex misidentification for both species, although only for shortspine thornyheads was the difference significant (in August).

The differences in sex misidentification among geographic areas are more difficult to explain. Sex of longspine thornyhead was more frequently misidentified in the U.S.-Vancouver and Columbia areas. Samples in these areas were collected primarily in June and September, the periods with the highest rates of sex misidentification. The lack of any significant differences in mean length for longspine thornyheads between INPFC areas indicates that the higher rates of misidentification of sex farther north were not a function of size, but were related to the timing of the annual spawning cycle at differing latitudes.

Shortspine thornyhead samples collected in the Eureka, Columbia, and U.S.-Vancouver areas (i.e., those with significantly lower rates of sex misidentification) were primarily taken in June, July, and September when the rate of sex misidentification for shortspine thornyheads was lowest. Additionally, there were significant differences in the lengths of shortspine thornyheads among areas, indicating that the lower rates of sex misidentification in the U.S.-Vancouver area may also be partially related to size (although similar size differences were not observed in the Eureka and Columbia areas). Because differences in geographic area were related to size for at least one thornyhead species and the differences in seasonal determination of sex were variable, we recommend that sex determination of thornyheads <18 cm not be attempted in the field. This is likely a conservative estimate because identifying sex in fresh specimens at sea is somewhat more reliable than examining frozen and thawed specimens in the laboratory. The approach described here establishes a protocol for determining a minimum size for at-sea sex identification of thornyheads, but may be applicable for use with any species where ambiguity may exist in correctly identifying the sex of fish at smaller sizes, within different regions, or across spawning or other seasonal cycles.

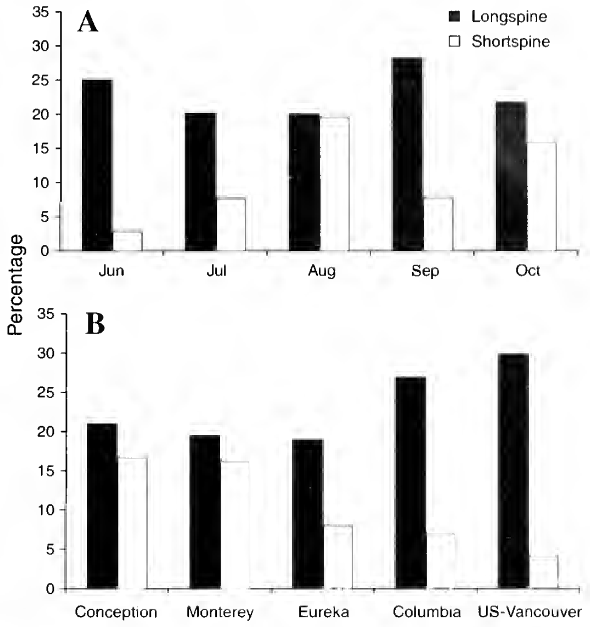

Figure 3

Percentage of sex-misidentified longspine (*Sebastolobus altivelis*) and shortspine (*Sebastolobus alascanus*) thornyheads determined by comparing the gross morphological features of gonads to a section of each gonad subsequently stained and viewed microscopically (**A**) by month, and (**B**) by geographic area as defined by the International North Pacific Fisheries Commission regions: Conception (U.S.-Mexico border to 36°00′N lat.), Monterey (36°00′ to 40°30′N lat.), Eureka (40°30′ to 43°00′N lat.), Columbia (43°00′ to 47°30′N lat.), and U.S.-Vancouver (47°30′N lat. to U.S.-Canada border).

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Measurement errors in body size of sea scallops (*Placopecten magellanicus*) and their effect on stock assessment models

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Abstract—Body-size measurement errors are usually ignored in stock assessments, but may be important when body-size data (e.g., from visual surveys) are imprecise. We used experiments and models to quantify measurement errors and their effects on assessment models for sea scallops (*Placopecten magellanicus*). Errors in size data obscured modes from strong year classes and increased frequency and size of the largest and smallest sizes, potentially biasing growth, mortality, and biomass estimates. Modeling techniques for errors in age data proved useful for errors in size data. In terms of a goodness of model fit to the assessment data, it was more important to accommodate variance than bias. Models that accommodated size errors fitted size data substantially better. We recommend experimental quantification of errors along with a modeling approach that accommodates measurement errors because a direct algebraic approach was not robust and because error parameters were difficult to estimate in our assessment model. The importance of measurement errors depends on many factors and should be evaluated on a case by case basis.

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Two fishery-independent surveys are important for monitoring Atlantic sea scallop (*Placopecten magellanicus*) abundance and biomass levels off the northeastern coast of the United States because they provide abundance, body size,[1] meat weight (weight of marketable adductor muscles), and other data (NEFSC[2,3]). The National Marine Fisheries Service, Northeast Fisheries Science Center (NEFSC) sea scallop dredge survey has been conducted annually since 1977 (Serchuk et al., 1979; Serchuk and Wigley, 1986). In addition, an underwater video survey for sea scallops and other benthic organisms has been conducted annually since 2003 (Stokesbury, 2002; Stokesbury et al., 2004) by the University of Massachusetts Dartmouth, School for Marine Science and Technology (SMAST). The dredge and video surveys are carried out across the range of sea scallops in U.S. waters.

In this analysis, we used sea scallops to draw attention to errors in body-size data when the data are used in a length-structured stock assessment model. The topic of measurement errors in body-size data has received relatively little attention, although Heery and Berkson (2009) evaluated effects of systematic errors (biased sampling) in fishery size-composition data used in an age-structured model. Our work was motivated by questions that arose from examining video survey shell-height data in sea scallop stock assessments (NEFSC[2,3]). Our experimental and analytical results may be important and useful in other situations where body-size data are imprecise. Body-

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[1] Shell height (SH, the distance in mm between the umbo and shell margin) is the body size measurement for sea scallops.

[2] NEFSC (Northeast Fisheries Science Center). 2004. Stock assessment for Atlantic sea scallops. *In* 39th northeast regional stock assessment workshop (39th SAW) assessment summary report and assessment report. Northeast Fisheries Science Center, National Marine Fisheries Service, Woods Hole Laboratory, 166 Water St., Woods Hole, MA 02543. Ref. Doc. 04-10, p. 87–211.

[3] NEFSC (Northeast Fisheries Science Center). 2007. Stock assessment for Atlantic sea scallops. *In* 45th northeast regional stock assessment workshop (45th SAW) assessment summary report and assessment report. Northeast Fisheries Science Center, National Marine Fisheries Service, Woods Hole Laboratory, 166 Water St., Woods Hole, MA 02543. Ref. Doc. 07-16, p. 139-370.

size data may be imprecise, for example, when collected by scuba (St. John et al., 1990; Edgar et al., 2004), remotely operated underwater vehicles (ROV; Butler et al., 2006), camera sleds (Rosenkranz and Byersdorfer, 2004), or in other optical surveys where body-size measurements are obtained without handling individual specimens.

In fishery stock assessment modeling, body-size measurements are almost always assumed to be without error. In contrast, statistical sampling errors that arise from too few are often considered in modeling (Fournier and Archibald, 1982; Pennington et al., 2001). Measurement errors in fishery age data have received substantial attention and are often addressed in stock assessment modeling (Methot, 1989, 1990). Approaches to dealing with measurement error in body-size data have not been explored.

Shell-height composition data for sea scallops are of two types: 1) distributions of shell-height measurements, which include measurement errors and true variability among individuals in size; and 2) distributions of shell-height measurements, which include measurement errors only. It is important to distinguish between these two types of data. In particular, shell-height compositions are sample specific and depend on the underlying distribution of true sizes. In our study measurement errors are the difference between the video or board measurements and the true shell height of individual specimens (i.e., after removing differences in true shell height among individuals). Shell-height composition data are important because they are interpreted in stock assessments to estimate year-class strength, mortality, and other biological characteristics. In our study measurement errors are important because they can be used to quantify the accuracy of the measurement process itself and because they affect shell-height data from all samples.

Two types of measurement errors are considered in this study. The first type is bias that causes individual shell-height measurements and estimated sample means to differ, on average, from their true values (Cochran, 1977). The second type is random errors, which cause variability in shell-height measurements and affect the precision of measurements and estimated mean values (Cochran, 1977).

Figure 1 shows how hypothetical errors in sea scallop shell-height measurements tend to smooth the true underlying distribution of the data. Measurement errors tend to smooth modes in the data (which usually correspond to recruitment events) by moving individuals from size bins with relatively high numbers into adjacent bins with lower numbers. Random measurement errors also tend to expand the range of observed sizes by decreasing the smallest observed size and increasing the largest (Fig. 1). Bias degrades body-size data by making measurements consistently larger or smaller than the true value. Methot (1989, 1990) highlighted these issues in the context of age data from survey and fishery samples. We use Methot's modeling methods in our analysis for shell-height data.

In principal, body-size measurement errors can cause errors in a wide range of important fishery estimates but biomass estimates are of particular importance. In the absence of bias, imprecise body-size data tend to cause positive bias in mean weight and biomass estimates because of the nonlinear relationship between size and biomass and Jensen's inequality (Feller, 1966). For example, according to Jensen's inequality, if body weight is a cubic function of body size, then a −10% error in body size will cause a $0.9^3-1 = -27\%$ error in estimated body weight for one individual. In contrast, a +10% error in body size will cause a $1.1^3-1 = +33\%$ error in body weight. The combined effect of the two errors for two scallops of the same size would be a positive bias of +6%.

The length-based Beverton-Holt mortality estimator involves equilibrium and other assumptions that may make it inappropriate to use in some cases (Gedamke and Hoenig, 2006), but it clearly demonstrates the potential effects of errors in body-size measurements on stock assessment model mortality estimates:

$$Z = \frac{K\left(L_\infty - \bar{L}\right)}{\bar{L} - L_c}, \tag{1}$$

where Z = the instantaneous rate of mortality from all sources;
L_∞ = asymptotic length;
K = rate parameter from the von Bertalanffy growth equation;
$\bar{L}$ = average length of individuals in a sample from the fishery; and
L_c = the "critical" length at which individuals are fully vulnerable to the fishery (Quinn and Deriso, 1999).

With all other factors held constant, a positive bias in $\bar{L}$ will make the numerator in Equation 1 too small, the denominator too large, and the mortality estimate will be biased low. Conversely, a negative bias in $\bar{L}$ will bias the mortality estimate high.

In this article, we characterize measurement errors in shell-height data for sea scallops in two types of surveys, using experimental data. The experimental results are used to evaluate effects on mean body weight and swept-area biomass estimates, and on biomass and mortality estimates from a modern size-structured stock assessment model. The assessment model demonstrates a promising approach (used originally for age data) for accommodating measurement errors in body-size data. In the appendices, we use numerical and bootstrap techniques to evaluate robustness of the assessment model approach in comparison to an algebraic one. Our purpose is not to evaluate the merits of any particular survey, rather, we use sea scallops as an example for dealing with general problems arising from body-size measurement errors in survey and fishery-dependent data, and for suggesting possible approaches to using such data.

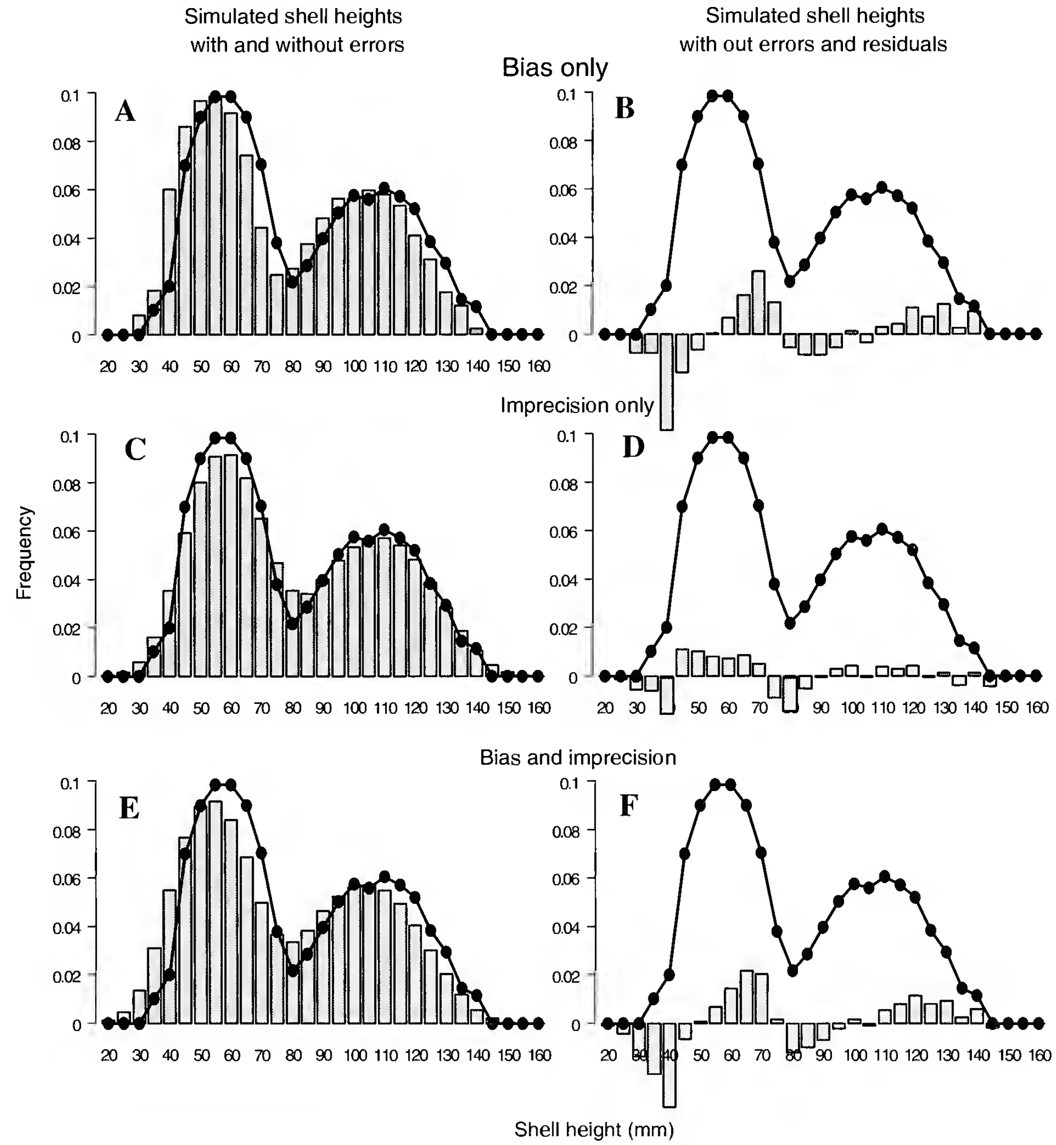

Figure 1

Rootograms (Tukey, 1977) showing hypothetical distributions of Atlantic sea scallop (*Placopecten magellanicus*) shell-height (SH) measurements with and without simulated measurement errors. The black line in each panel shows the distribution of measurements with no errors (5-mm size bins). In the left column, bars show distributions of shell heights with measurement errors. In the right column, bars show residuals (measurement with no errors minus measurements with errors). For the "bias only" scenario (**A** and **B**), precise measurement errors were assumed with a bias of −4.1 mm. For the "imprecision only" scenario (**C** and **D**) unbiased measurement errors were assumed with a standard deviation of 6.1 mm. For the "imprecision and bias" scenario (**E** and **F**), measurement errors were assumed with a bias of −4.1 mm and standard deviation of 6.1 mm.

Materials and methods

The SMAST sea scallop survey is conducted with video cameras mounted on a steel pyramid frame to provide a 3.24-m^2 view of the sea floor and associated macrobenthos (Stokesbury, 2002; Stokesbury et al., 2004). Video images are recorded at sea on high-resolution S-VHS videotape and then replayed in the laboratory where digitized images are created. All sea scallops are counted, and all clearly visible sea scallops (with the hinge and opposite edge visible) within the digitized images are measured to the nearest mm by using Image Pro Plus® software (Media Cybernetics, Inc., Bethesda, MD).

In previous analyses, correction factors were applied to the raw video shell-height measurements to account for distance from the origin (DFO), which is the distance of a specimen from the "origin" (center) of the sampling frame (Stokesbury et al., 2004). Subsequent work during routine stock assessments (unpublished) indicated that adjustments were unnecessary because the distributions of measurement errors were simpler and easier to describe statistically, and data were easier to model without adjustments. Moreover, adjusted data were sometimes less accurate than the unadjusted data. Additional research may result in more accurate adjustments or transformations of body-size data. However, unadjusted video data from the "large" camera on the sampling frame are used in current stock assessments and in this analysis.

NEFSC sea scallop surveys are conducted with a 2.44-m New Bedford sea scallop dredge with a 38-mm liner. The catch is sorted, counted, and measured on the deck of the research vessel. In most cases, the entire catch is counted and measured, but a few large catches were subsampled. During the early 1980s through 2003, sea scallops in the catch were measured to the nearest 5-mm shell-height interval with a standard NEFSC sea scallop measuring board.

Experiments

Two experiments were conducted during 20 and 23 February 2003 when the SMAST video pyramid was placed in a 341,000-L tank filled with seawater in the SMAST laboratory. NEFSC sea scallop measuring boards and SMAST video equipment in the experiments were configured and used in a realistic manner that was similar to use during actual surveys at sea. Accurate measurements used as true shell heights in this analysis were made to the nearest mm by using scientific calipers under laboratory conditions with adequate lighting.

We used the experimental data to evaluate statistical characteristics of shell-height composition data and shell-height measurement errors.

Accuracy, bias, and precision of measurements were quantified by comparing data obtained from the measuring board and video camera with data from the caliper. Accuracy is the closeness to the true underlying value and is measured by mean square error (MSE). For shell-height composition data,

$$MSE = \left(\bar{h} - \bar{H}\right)^2, \qquad (2)$$

where $\bar{h}$ = the mean of the measurements; and
$\bar{H}$ = the mean of the true values for the sample (Cochran, 1977).

For measurement errors in our analysis,

$$MSE = \frac{\sum_{j=1}^{n} e_j^2}{n}, \qquad (3)$$

where $e_j = h_j - H_j$ = the error for the j^{th} observation (where h_j is the measurement and H_j is the true value).

Bias and variance both contribute to MSE. In fact, MSE = $s^2 + b^2$, where s^2 is the variance and b is bias (Cochran, 1977). In our study, $b = \bar{h} - \bar{H}$ where $\bar{h}$ is the mean of shell-height measurements and $\bar{H}$ is the mean of the true shell heights in the sample. Bias is the same for shell-height composition data and measurement errors as shown below:

$$\sum_{j=1}^{n}\left(h_j - H_j\right)/n = \bar{h} - \bar{H}. \qquad (4)$$

Variance (s^2) was computed from shell-height composition data or measurement errors by using the standard formula. Variance of shell-height composition data and measurement errors will generally be different because true shell heights usually differ among specimens in a sample.

It is convenient to express accuracy, bias, and precision in terms of the square root of the MSE (RMSE), bias (b), and standard deviation (s) because all three are absolute measures with the same units (mm for sea scallop shell-height data). Percent RMSE ($RMSE/h_{true}$), percent bias (b/h_{true}), and the CV ($s/\bar{h}$) are useful for making comparisons on a relative basis.

The third and fourth moment statistics, g_1 and g_2, were used to measure skewness (asymmetry) and kurtosis (peakedness) of shell-height composition data and measurement errors, in relation to what would be expected from a normal distribution (Sokal and Rohlf, 1995). Skewness and kurtosis statistics for shell-height composition data and measurement errors from the same sample differ if there is variability in size among specimens. For normally distributed random variables with no skewness, $g_1 = 0$. Negative g_1 values indicate skewness to the left (a distribution with a long left tail and more small values than expected in a normal distribution). Positive g_1 values indicate skewness to the right (long right tail with more large values than expected). Similarly, positive g_2 values indicate distributions more peaked than expected for a normal distribution, and negative g_2 values indicate distributions that are less peaked (flatter) than expected. The two statistics convey information about the shape of any distribution in relation to a normal distribution, but care is required in interpreting g_1 and g_2, particularly for data that are far from normally distributed. The skewness and kurtosis statistics were easier to interpret for measurement errors than for shell-height measurements because the latter were not normally distributed.

We used a test for normally distributed statistics (Sokal and Rohlf, 1995) to evaluate the statistical significance of skewness and kurtosis for distributions of measurement errors that might be otherwise assumed normally distributed. Statistical tests were carried out for distributions of measurement errors because they were closer to normally distributed.

Multiple shell height-measurements were usually made from single specimens in our experiments. We made allowance for repeated sampling when testing skewness and kurtosis by using the number of unique specimens in the experiment as the degrees of freedom instead of the number of measurements (i.e., if n measurements were made on each of k specimens, we used k as the degrees of freedom in statistical tests). The effect of this adjustment was to make the statistical tests more conservative (less likely to reject the null hypothesis of no difference). The number of specimens is a reasonable lower bound estimate of the true effective sample size.

Body weights for sea scallops and other marine organisms are often computed from body size. For sea scallops in this analysis,

$$W = e^{\alpha+\beta \ln(h)}, \tag{5}$$

where W = sea scallop meat weight (g, the weight of the marketable adductor muscle);
h = shell height (mm); and the parameter values α=–12.01 and β=3.22.

Bland-Altman plots (1986, 1995) were used to characterize shell-height measurement errors. In the case of measuring boards, for example, the difference between the measuring board and caliper shell-height measurements for each sea scallop was plotted on the y-axis against the average of the two measures for the same individual on the x-axis. Bland-Altman plots are typically presented as scatter plots with a point for each difference (pair of measurements); however, boxplots may be more useful in some circumstances (see below). Bland-Altman plots are useful because they eliminate spurious correlations when the difference of y–x is plotted against the more precise measure (x) and because patterns are easier to discern along a horizontal line (the x-axis) than along a diagonal line. Spurious correlations occur because the measurement error in x affects the variables plotted on both the x- and y-axes.

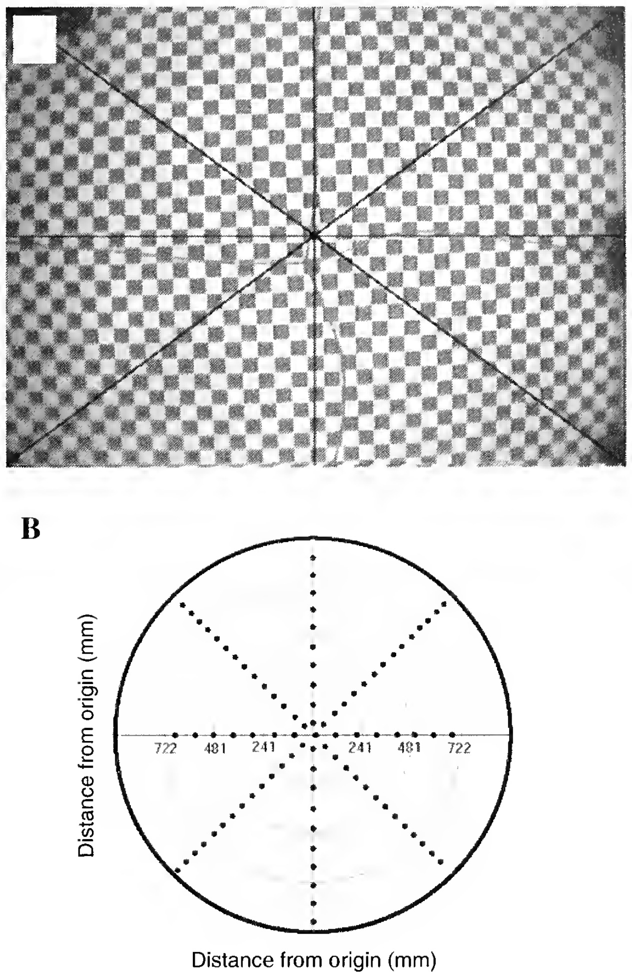

Figure 2

(**A**) A video image showing ceramic tiles under water in the tank where they were placed for experiment 1. (**B**) Dots show the locations of the 91 tiles in the video images that were measured in experiment 1. The height, width, horizontal and vertical distance from the origin (DFO) was recorded for each tile measured. The x- and y-axis are the same in the top and bottom panels.

Experiment 1 was designed to measure the accuracy of video measurements for objects of known size (square ceramic tiles) as a function of position in the video frame as measured by DFO (Fig. 2). Scuba divers in experiment 1 placed black and white ceramic floor tiles (all were 48.5×48.5 mm) in a closely packed square grid on the bottom of the tank, starting at the center of the video pyramid and covering the entire range of view in actual surveys (Fig. 2). The width and height of 91 tiles across the field of view and at various distances and positions from the center of the sampling frame (Fig. 2) were estimated from video images by using the standard video survey procedures described above. Data were recorded in such a way that the length and height measurements from the same tile could be associated with each other and with the particular position of the tile in the video image. The tiles used in experiment 1 (48.5×48.5 mm) corresponded roughly with the size of the smallest scallops fully recruited to the dredge and video surveys (about 40 mm SH) and included in stock assessment analyses. Sea scallops, according to actual survey data, cover a much wider range of shell heights (to about 190 mm SH in experiment 2, see *Discussion* section).

Experiment 2 was designed to measure the accuracy of video shell-height measurements for sea scallop shells of varying sizes (39 to 192 mm SH) placed randomly on a sand-granule-pebble substrate, similar to the random aggregations observed on Georges Bank. All shell-height measurements could be linked with each individual sea scallop in experiment 2 because the right valve of 172 individual sea scallop shells was numbered uniquely. The identification numbers were large and written under the valve with dark indelible ink and clearly visible with video equipment when the sea scallops were turned over so that the labels faced the camera. The numbered sea scallops were assigned randomly to fifteen groups. All members of the same group were stored together in a bag with a unique label for group identification.

In each experimental replicate, a group of shell valves was placed randomly on the bottom of the tank. Two video images were made for each group. The first image (with the valve turned towards the sediment and identification numbers hidden) was used by four technicians to independently measure shell heights. The second image was taken with identification numbers visible after divers turned the shells over and replaced them in their original positions. After video images were recorded, the shell valves were measured with measuring boards by two technicians who could not see the identification numbers and once by a third technician with calipers.

A stock assessment model that incorporates errors from shell-height measurements

Following NEFSC[2,3] procedures, we used results from experiment 2 and a modified version of the CASA (catch-at-size-analysis, Sullivan et al., 1990) stock assessment model (Appendix 1) to investigate potential effects of shell-height measurement errors on model-based biomass and fishing mortality estimates for two sea scallop stocks. Assessment model results in this article should not be used by managers because model runs were tailored to investigate potential effects of shell-height measurement errors and because some types of data were omitted.

As described in Appendix 1, the CASA model that is routinely used for sea scallop stock assessments accommodates both bias and imprecision in shell-height measurements. CASA models were run for sea scallops in the Mid-Atlantic Bight during 1982–2006. In contrast to NEFSC[2], measurement error parameters were obtained from experiments and not estimated in the CASA model itself. The data used in modeling included commercial landings in metric tons (t), survey trend data (numbers per unit of sampling effort) from the camera video and dredge surveys, and shell-height composition data from the commercial fishery, video, and dredge surveys. Survey selectivity patterns were not estimated because the video and dredge surveys have flat selectivity patterns (catch sea scallops equally well) at shell height ≥40 mm, and goodness-of-fit calculations were restricted to this size range (Appendices B7–B8 in NEFSC[3]). Measurement errors in commercial shell-height data were assumed to be the same as those in the dredge survey for lack of better information and because procedures for measuring sea scallops on land in port samples and at-sea in fishery observer samples are similar to procedures followed in surveys.

As described in Appendix 1, bias and precision of shell-height measurements are represented in the CASA model by an error matrix (E) that gives the probability that a sea scallop in each true shell-height bin is assigned to a range of observed shell-height bins (a range that accommodates measurement errors). As described by Methot (1989, 1990) for age data, the error matrix E can be set up to deal with a wide range of situations for bias and variance (e.g., both can vary among shell-height bins or over time).

For the calculation of E for sea scallops in this analysis, shell-height measurement error distributions were assumed to be normally distributed with means and standard deviations from experiment 2. The normal distributions for measurement errors were truncated three standard deviations above and below the mean. In calculating distributions of measurement errors, true shell heights were assumed with or without bias to be uniformly distributed within each true 5-mm SH bin so that, for example, the frequency of sea scallops with true shell heights of 70, 71, 72, 73, and 74 mm (in the 70–74.9 mm SH bin with midpoint 72.5) was the same. Distributions for measurement errors were normalized to sum to one before use in the CASA model.

Results

Height and width measurements from the same tiles in experiment 1 were not significantly different by a paired t-test ($t=-0.23$, $P=0.30$, 91 df). Therefore, height and width measurements from 91 tiles in experiment 1 were combined to form a single set of video data (a total of 182 measurements) (Table 1).

The RMSE statistic for video tile-size composition and measurement errors in experiment 1 (Table 1) was 3.5 mm (%RMSE=7%, Table 1). Bias (−2.2 mm) and imprecision (standard deviation 2.7 mm) of video tile measurements were similar. In comparison to the true size of the tiles (48.5 mm), the smallest measurement was 38 mm, and the largest measurement was 50 mm. The video size-composition data and measurement errors were left skewed ($g_1=-0.28$) and flatter ($g_2=-0.53$) than expected for a normal distribution. There were gaps in the distribution of the video tile measurements (Fig. 3) due to the resolution of the video images used in digitizing (each pixel≈3 × 3 mm).

Measurement error increased with DFO for the video tile measurements (Fig. 3). Bias was positive for DFO <400 mm and negative at larger DFO levels.

RMSE for shell-height composition data in experiment 2 was 33 mm (%RMSE 30%) for video and 34 mm (%RMSE=31%) for measuring board data (Table 2). Mean shell height was 106 mm for video and 109 mm for measuring boards, compared to 110 mm for calipers. Minimum shell height was 34 mm for video, 38 mm for measuring boards, and 39 mm for calipers. Maximum shell height was 201 mm for video, 193 mm for measuring boards, and 192 mm for calipers.

Bland-Altman plots for experiment 2 show that measuring board shell heights were more accurate than video measurements, and that bias in video and measuring board data was relatively constant across the range of shell heights in experiment 2 (Fig. 4). However, relatively large outliers sometimes occurred in video measurements at 80–130 mm SH (Fig. 4).

Video and measuring-board shell-height compositions in experiment 2 were similar in terms of skewness with g_1=−0.41 for video measurements and −0.47 for measuring boards compared to −0.46 for calipers (Table 2). The video shell-height distribution was more peaked with g_2=−0.65 compared to g_2=−0.85 for measuring boards, and g_2=−0.84 for calipers (Table 2). Video measurement errors were skewed to the left (g_1=−0.60) compared to measuring-board errors which were nearly symmetrical (g_1=−0.05). The distribution of errors for measuring boards was flatter (g_2=−0.85) and video measurement errors were more peaked (g_2=1.84) than would be expected for normal distribution. The error distribution for measuring boards had a nearly flat mode about 5-mm wide because shell heights are automatically truncated by measuring boards to the next lowest 5-mm shell-height bin.

On a proportional basis, meat weights calculated from shell heights in experiment 2 were much less accurate than the original shell-height measurements. In particular, %RMSE values for meat weights were 71% and 74% for video and measuring boards, respectively (Table 3), compared to 30% and 31% for the original

Table 1

Summary of size-composition data and measurement errors for 182 tile measurements (height and width from 91 tiles, each 48.5×48.5 mm) by video equipment in experiment 1.

Statistic	Video
Measurements and measurement errors	
Bias	−2.2
Standard deviation	2.7
Square root of the mean squared error	3.5
Skewness (g_1)	−0.28
Kurtosis (g_2)	−0.53
Measurements	
Minimum	38.3
5% quantile	41.2
95% quantile	50.1
Maximum	50.1
Average	46.3
Percent bias	−5%
Coefficient of variation	6%
Percent square root of the mean squared error	7%

Table 2

Summary statistics for shell-height composition data and measurement errors (in mm) from 172 uniquely identified Atlantic sea scallop (*Placopecten magellanicus*) shell valves in experiment 2. "NA" means that a statistic is not applicable.

Statistic	True shell height (calipers)	Video	Measuring boards
Shell heights and measurement errors			
n measurements used	172	670	344
n omitted	0	18	0
Bias	NA	−4.5	−0.6
Shell heights			
Minimum	38.5	34.3	37.5
5% quantile	54.8	48.8	52.5
95% quantile	149.6	147.3	147.5
Maximum	192.0	200.6	192.5
Average	109.9	106.5	109.3
Percent bias	NA	−4%	−1%
Standard deviation	33.5	33.1	33.6
Coefficient of variation	30%	31%	31%
Square root of the mean squared error	NA	33.4	33.6
Percent square root of the mean squared error	NA	30%	31%
Skewness (g_1)	−0.46	−0.41	−0.47
Kurtosis (g_2)	−0.84	−0.65	−0.85
Measurement errors			
Standard deviation	NA	6.1	1.7
Square root of the mean squared error	NA	7.6	1.8
Skewness (g_1)	NA	−0.60	−0.044
Kurtosis (g_2)	NA	1.84	−0.85

shell heights (Table 2). The nonlinear shell-height to meat-weight relationship showed exaggerated extremes of the distributions so that the ratio of maximum to mean meat weight was 158/27=5.9 for video data and 138/29=4.8 for measuring boards (Table 3) compared to 201/106=1.9 and 193/109=1.8 for shell heights (Table 2). Variance in meat-weight measurements increases as true meat-weight increases for video data and, to a lesser extent, for measuring boards (Fig. 5).

The meat-weight composition data were more right skewed (g_1=1.53) and flatter (g_2=6.22) than the meat-weight composition data from measuring boards (g_1=0.92 and g_2=2.61) or calipers (g_1=0.99 and g_2=3.00). Errors in meat-weight data were left skewed and not as peaked for video (g_1=–0.80 and g_2=2.48) than measuring board data (g_1=–1.06 and g_2=4.68).

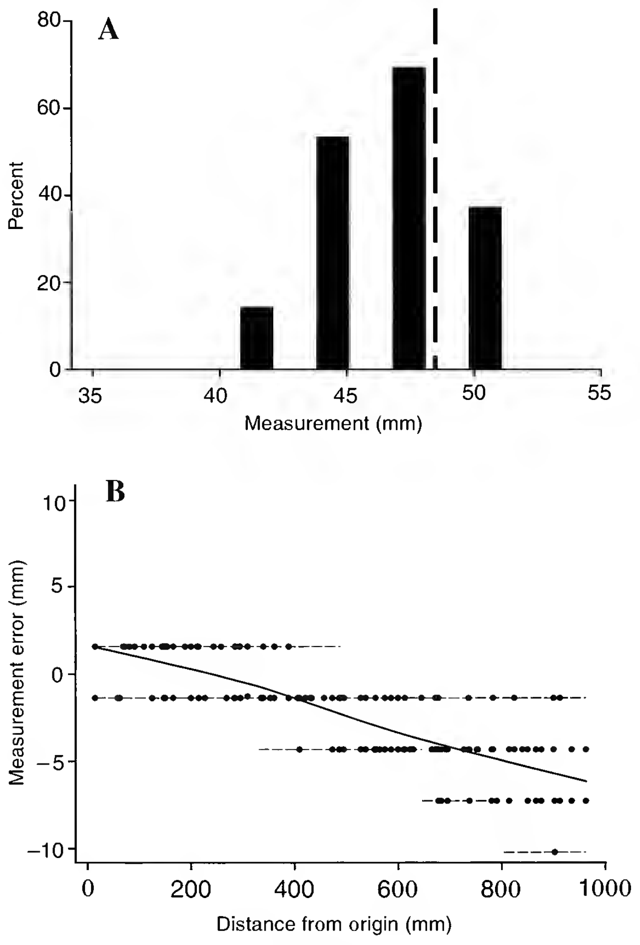

Figure 3

(A) Video measurements for tiles in experiment 1. The vertical line shows the true value at 48.5 mm. (**B**) Measurement errors (video measurement minus caliper measurement) for tiles in experiment 1 as a function of distance from the origin (DFO). The nonlinear LOESS regression line shows the overall trend in measurement errors as a function of DFO.

Results from the assessment models

Based on results from experiment 2 (Table 2) and assumptions listed above, video shell-height measurements for sea scallops with true sizes evenly distributed over 100–104.99 mm SH (i.e., the 100-mm bin with midpoint 102.5 mm) would fall into nine observed shell-height bins with midpoints from 77.5 to 117.5 mm (Table 4). Measuring board shell-height measurements would fall into four observed shell-height bins with midpoints ranging from 92.5 to 107.5 mm (Table 4).

Four model configurations were used. The "no measurement error" model configuration was fitted by assuming no errors in shell-height data. The "bias only" model was fitted by assuming that shell-height data were biased (to the extent measured in experiment 2), but precise (with zero variance). The "imprecision only" model was fitted by assuming that shell-height measurements were imprecise (standard deviations from experiment 2), but not biased. The "imprecision and bias" model was fitted by assuming both types of shell-height measurement errors.

Models which accommodated measurement errors fitted better, with substantially lower negative log likelihoods for both stocks, than models that ignored measurement errors. Differences in negative log likelihood were mostly for shell-height composition data. Mean 2004–06 biomass and fishing mortality rates and coefficients of variation (CV) for biomass and fishing mortality estimates were similar for all model configurations (Table 5).

Discussion

The importance of body-size measurement errors and the need to accommodate them in modeling probably depends on the situation. Biological factors (growth rate, recruitment variability), assessment model type, quality and quantity of fishery and fishery-independent data may be important. Sea scallops may be an atypical case because they are a data-rich species. We suggest that the potential importance of body size measurement errors should be evaluated on a case by case basis, particularly if body-size data may be imprecise or biased. Simulation studies may be useful in determining the importance of experimentally derived body-size measurement errors on stock assessment results.

In the sea scallop case, models that accommodated measurement errors fitted substantially better, but there was little effect on point estimates and variances for recent biomass and fishing mortality. We hypothesize that effects on biomass and mortality estimates would be larger in cases with positive biases in body-size measurements. For both video and measuring boards, the positive bias in meat weights due to the nonlinear relationship between body size and meat weight was mitigated to some extent by the negative bias in shell-height measurements. In contrast, Heery and Berkson (2009) used simulations to evaluate effects of systematic sampling errors (too many small or too many large individuals) in size-composition data from commercial catches and three simulated stocks. The simulated data were used in a forward-projecting age-structured stock assessment and in projection models to estimate stock size and fishing mortality in relation to threshold values, and rebuilding trajectories. Body-size data with too many large individuals biased stock size high and fishing mortality low and tended to support management measures that did not meet management goals, particularly for longer lived and depleted stocks. Body-size data with too many small individuals were less problematic, but tended to support overly restrictive management actions in extreme cases. Heery and Berkson's (2009) results indicate that systematic errors in sampling may be more important than errors in individual measurements of body size.

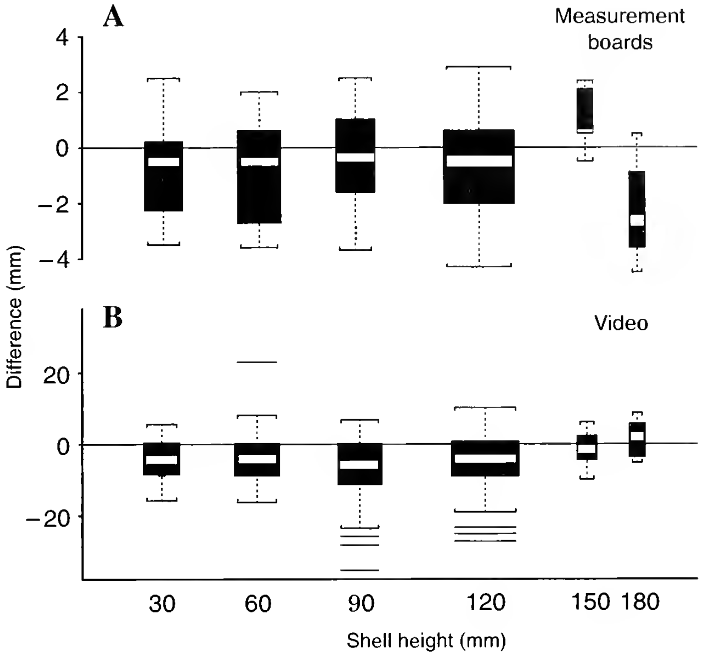

Figure 4

Modified Bland-Altman plots for Atlantic sea scallop (*Placopecten magellanicus*) shell-height (SH) measurements in experiment 2. The y-axis shows the difference between the experimental measurement (measuring boards in **A** or video in **B**) and the caliper measurement. The x-axis shows the average of the experimental and caliper measurement. Boxplots and 30-mm shell-height bins were used instead of traditional scatter plots for shell height measurements in experiment 2 because the large number of samples between 120 and 150 mm SH gave the impression that variance was higher for those sizes. Boxplots show the interquartile range (a robust variance measure) and are not sensitive to sample size. The width of the boxplots is proportional to the number of observations for the shell-height bin.

Variance in calculated meat weights increased rapidly with shell height with both video and measuring board techniques, in contrast to the variance in shell heights (Figs. 4 and 5). This additional source of variability likely increases variance in biomass estimates, particularly for relatively large fishable sea scallops.

In our analysis, assessment models that accommodated shell-height measurement errors fitted better, even though no additional parameters were estimated. The Mid-Atlantic Bight model that accommodated imprecise (but not biased) shell-height measurement errors had a negative log likelihood that was 15 units smaller than the negative log likelihood for the no measurement error model (Table 5). Results for the Georges Bank stock (not shown to conserve space) were similar. In contrast and based on likelihood theory, a difference in negative log likelihoods of just 1.92 units is sufficient to justify an additional parameter in a statistical model at the $P=0.05$ level (Venzon and Moolgavkar, 1988). Comparing results of the "bias only" scenario to results from the "imprecision only" and "imprecision and bias" scenarios, we found that improvements in goodness of fit were mostly due to accommodating imprecision; bias was less important (Table 5).

Experiments

Our results highlight the value and information that may be gained from evaluating body size measurement errors experimentally. Body-size measurement error experiments should be conducted when survey equipment is changed, particularly if body-size measurements are imprecise. In some cases, frequent "mini-experiments" may be required if the accuracy of the equipment tends to drift over time or change in response to environmental conditions.

Our results indicate the importance of designing measurement error experiments so that individual specimens can be identified and associated with individual measurements; otherwise measurement errors can not be estimated individually and evaluated directly. Data from experiment 2 were most useful because individual sea scallops were numbered and replicate measurements of different types could be linked and analyzed in detail. In addition, the full range of variability for all important factors (i.e., distance from the origin (DFO), shell height, and identity of individual technicians) should be included in the experimental design.

We ignored skewness and kurtosis in measurement errors in calculating measurement error matrices for use in the CASA stock assessment model. In future modeling, it may be better to use the experimental dis-

Table 3

Summary statistics of meat weights and meat weight measurement errors (g) for Atlantic sea scallop (*Placopecten magellanicus*) shell-height measurements in experiment 2 (sample sizes are the same as those for shell-height measurements in Table 2). The original shell heights were obtained with calipers, video camera, and measure boards. "NA" means that a statistic is not applicable.

Statistic	True (calipers)	Video	Measuring boards
Meat weights and measurement errors			
Bias	NA	–3.2	–0.4
Meat weights			
Minimum	0.8	0.5	0.7
5% quantile	2.4	1.7	2.1
95% quantile	61.3	58.3	58.6
Maximum	136.9	157.7	138.0
Average	29.8	27.3	29.4
Percent bias	NA	–10%	–1%
Standard deviation	22.2	21.4	21.8
Coefficient of deviation	74%	78%	74%
Square root of the mean squared error	NA	21.6	21.8
Percent square root of the mean squared error	NA	71%	74%
Skewness (g_1)	0.99	1.53	0.92
Kurtosis (g_2)	3.00	6.22	2.61
Measurement errors			
Standard deviation	NA	5.1	1.5
Square root of the mean squared error	NA	6.0	1.6
Skewness (g_1)	NA	–0.80	–1.06
Kurtosis (g_2)	NA	2.48	4.68

Table 4

Estimated probability distributions for Atlantic sea scallop (*Placopecten magellanicus*) shell-height (SH) measurements based on bias and standard deviations from experiment 2. Condition factors for error matrices used in the catch-at-size-analysis (CASA) stock assessment model scenarios are given also. The shell-height bins are 5-mm wide and identified by their midpoint. For example, sea scallops 80–84.9 mm SH fall into a bin whose midpoint is 82.5 mm.

		Video scenario			Measuring board scenario		
Statistic	Calipers (true shell height)	Bias only	Imprecision only	Imprecision and bias	Bias only	Imprecision only	Imprecision and bias
Condition factor (κ)	NA	3×10^{15}	5457	2638	1.6	2.1	2.3
Bias (mm)	0	–4.5	0	–4.5	–0.6	0	–0.6
Standard deviation (mm)	0	0	6.1	6.1	0	1.7	1.7
Shell height bin (mm)	Probability of observed bins						
72.5							
77.5				0.0009			
82.5			0.0014	0.0167			
87.5			0.0203	0.0820			
92.5			0.0929	0.2158			0.0001
97.5		0.8000	0.2300	0.3101	0.2000	0.1325	0.2008
102.5	1.0000	0.2000	0.3110	0.2436	0.8000	0.7349	0.7181
107.5			0.2300	0.1045		0.1325	0.0810
112.5			0.0929	0.0243			
117.5			0.0203	0.0020			
122.5			0.0014				
127.5							

tributions of measurement errors directly in error matrices, particularly if experimental sample sizes are large.

Drouineau et al. (2008) used simulation analysis to show the importance of alternative assumptions about the distribution of individuals within size groups and the statistical distribution of growth increments in length-structured models like the CASA (catch-at-size-analysis) model. Our experience indicates that the same types of assumptions are important in calculating body-size measurement-error matrices. In particular, it was important to assume that individuals were uniformly distributed within size groups, to make realistic assumptions about the distributions of measurement errors, and to be careful in programming to ensure consistent calculations at the boundaries of length bins for calculating error matrices and for the stock assessment model.

Statistical methods for repeated measurements or random effects may be suitable for analysis of our experimental data. We made allowances for repeated measures in bootstrap calculations (Appendix 2) and in calculating P-values for skewness and kurtosis tests, but not in calculating other statistics (Tables 1–3).

Our experiments were conducted under ideal conditions with tiles and shell valves, rather than live sea scallops. Our results may underestimate the magnitude of errors under more realistic field conditions.

Model results may depend on shell-height bin width such that larger shell height bins would cause measurement errors to have a greater impact on biomass and mortality estimates. We used 5-mm SH bins for sea scallops because 5-mm is the resolution and approximate accuracy for the survey shell-height data. In general, it may be important to consider the magnitude of measurement errors in making decisions about size bins used in stock assessment modeling.

Body-size measurement errors

Random measurement errors are unavoidable. One may conclude that it is incumbent on the researcher to search out and correct sources of bias, whatever the source. We suggest that it may be more cost effective to quantify measurement errors experimentally and to accommodate them in modeling. Time series with consistent body-size measurement errors are probably easiest to interpret. Models may become overly complex if multiple sets of assumptions about measurement errors are required to interpret one survey time series. Resources required to quantify measurement errors after each adjustment to survey procedures or equipment may be better spent on more accurately characterizing the measurement errors for survey gear that remains the same for longer periods of time.

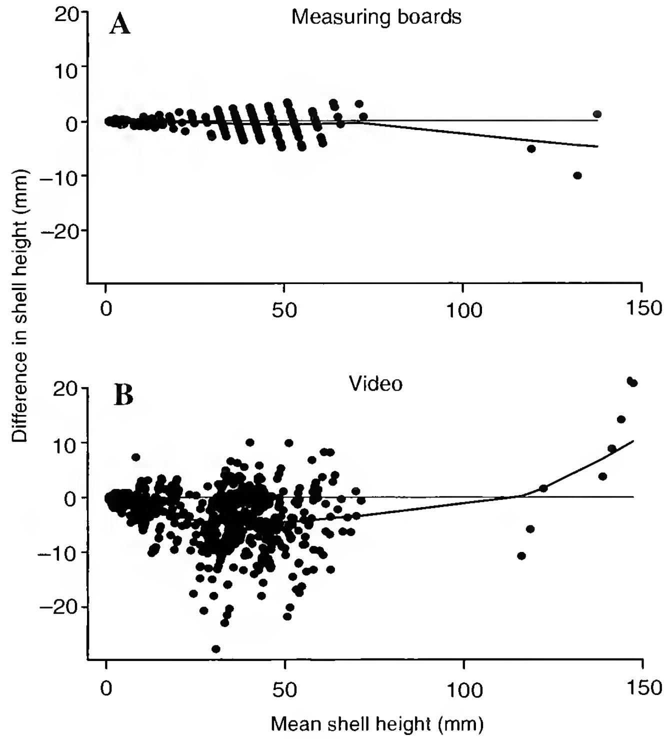

Figure 5

Bland-Altman plots for Atlantic sea scallop (*Placopecten magellanicus*) meat weights calculated from experimental shell-height measurements in experiment 2 (measuring boards in panel **A** and video in panel **B**). The y-axis shows the difference between the meat weights calculated from the experimental (video or measuring board) shell height measurements and the meat weights calculated from caliper measurements. The x-axis shows the average of the experimental and caliper-derived measurements.

Bootstrap results also showed that an algebraic approach to removing errors from the data by using the inverse error matrix E^{-1} gave negative proportions for both video and measuring board data in at least some size groups (Appendix 2). The sampling distribution for algebraically adjusted shell-height data may be difficult to characterize. These results indicate that it may be difficult to remove measurement errors directly from body-size data and we hypothesize that approaches like the one used in the CASA model will generally perform better. Bootstrap results showed that estimates of predicted shell-height composition data with measurement errors as carried out in the CASA model were robust to uncertainties in the measurement-error matrix E (Appendix 2). Models can be designed to be robust to measurement errors. For example, the last size bin in the CASA model is a plus-group that absorbs data for large scallops that may have been strongly affected by measurement errors. Other data in the model may have also contributed to the robustness of biomass and

Table 5

Results from the catch-at-size-analysis (CASA) model for Mid-Atlantic Bight sea scallops (*Placopecten magellanicus*) and four model configurations. The "no measurement error" model configuration does not accommodate shell-height measurement errors. Other model configurations accommodate bias and imprecise measurement errors in various combinations as shown in the table. Lower negative log likelihood (NLL) values indicate better model fit. Coefficients of variation (CV) shown in parenthesis are asymptotic variances calculated by the delta method. For ease of comparison, the "no measurement error" configuration NLL values were subtracted from corresponding NLL statistics for all three configurations. The lowest NLL, biomass or fishing mortality estimates in each row are printed in boldface.

Variable or estimate	No measurement error	Bias only	Imprecision only	Imprecision and bias
Bias and precision (mm) assumed in modeling				
Standard deviation—video survey	0.0	0.0	6.1	6.1
Bias—video survey	0.0	–4.5	0.0	–4.5
Standard deviation—dredge survey	0.0	0.0	1.7	1.7
Bias—survey	0.0	–0.6	0.0	–0.6
Negative log likelihood (NLL)				
Total	0.00	20.92	**–14.62**	–1.16
Commercial fishery shell-height data	0.00	4.99	**–0.34**	2.06
Dredge survey shell-height data	0.00	–4.14	**–10.66**	–6.97
Video survey shell-height data	0.00	19.45	–3.00	4.59
Mean biomass and fishing mortality during 2004–06				
Fishing mortality (*y*–1)	0.45	0.41	0.46	**0.42**
	(8%)	(7%)	(8%)	(8%)
Biomass (t meats)	81,211	84,650	**80,844**	83,602
	(5%)	(5%)	(5%)	(5%)

fishing mortality estimates to assumptions about shell-height measurement errors.

In principal, measurement-error parameters could be estimated directly in stock assessment models without resorting to experiments. Measurement-error parameters in the CASA model were estimated in the NEFSC study,[2] but the estimates proved to be unstable (NEFSC[3]). Without at least one source of accurate body-size data, there may be too little information about measurement errors to estimate parameters. In addition, there may be strong correlations between estimated measurement errors and estimates of other factors that affect interpretation of body-size data, such as survey and fishery selectivity, natural mortality, and recruitment variability.

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Appendix 1

Following the approach of the Northeast Fisheries Science Center (NEFSC,[2,3]) we used a likelihood approach to fitting the CASA model to sea scallop stock assessment data. The best estimates from the model minimized the combined negative log likelihood of all the data. Relevant details are described below. Appendix B10 in the NEFSC report (NEFSC[3]) is a complete technical description of the CASA model for sea scallops. Appendix B12 in that same report (NEFSC[3]) describes CASA model performance with simulated stock assessment data.

Estimates of population abundance and survey size selectivity are available for each shell height and year as the CASA model is fitted. In a single year, for example, we calculated the number of sea scallops in the population that were available or selected by the video gear with the following equation:

$$n_h = q_h N_h, \tag{A1}$$

where N_h = the predicted number of sea scallops in the population for shell height bin *h;*
q_h = the size-specific probability of detection (selectivity) in the video survey (on a scale of 0 to 1 and relative to the bin with maximum probability of detection); and
n_h = the estimated number of sea scallops in the population that are available to the video survey gear.

In the absence of measurement error, the predicted shell-height composition π_h for the survey is

$$\pi_h = \frac{n_h}{\sum_{i=1}^{L} n_i}, \tag{A2}$$

where L = the number of shell-height bins in the model.

If $\vec{\pi}$ is a row vector of length L containing the predicted proportions (before measurement errors) for each length group in the survey, then

$$\vec{p} = \vec{\pi} E, \tag{A3}$$

where $\vec{p}$ the row vector of predicted proportions (including measurement errors).

In Equation A3, E is a square measurement error matrix with L rows and columns that distributes numbers at true shell height into observed shell heights bins that are larger and smaller than the true shell height. For example, the first row of E sums to one and gives the probability of observed shell heights for sea scallops in the first true shell height bin. The last row of E sums to one and gives the probabilities that sea scallops in each shell height bin would be assigned to the "plus group" because of measurement error. As described in the text, we estimated E for sea scallops using results from experiment 2.

Appendix 2

Equation A3 in Appendix 1 indicates the possibility of correcting shell-height data measurement algebraically, without resorting to an approach like the CASA model. In particular, if the matrix E is invertible, then it may be possible to estimate the true sample proportions $\hat{\bar{\pi}}$ by multiplying both sides of Equation A3 by the inverse matrix E^{-1}:

$$\hat{\bar{\pi}} = \bar{p}E^{-1}. \qquad \text{(A4)}$$

However, the inverse calculation in Equation A4 will be unreliable if the estimated error matrix E is poorly conditioned. If the error matrix is poorly conditioned, then small inaccuracies in the estimate of E will propagate into larger errors in the inverse E^{-1} and the predicted proportions $\hat{\bar{\pi}}$.

As described by Horn and Johnson (1985), the condition factor for an invertible matrix E is

$$\kappa = \left\|E\right\| \left\|E^{-1}\right\|, \qquad \text{(A5)}$$

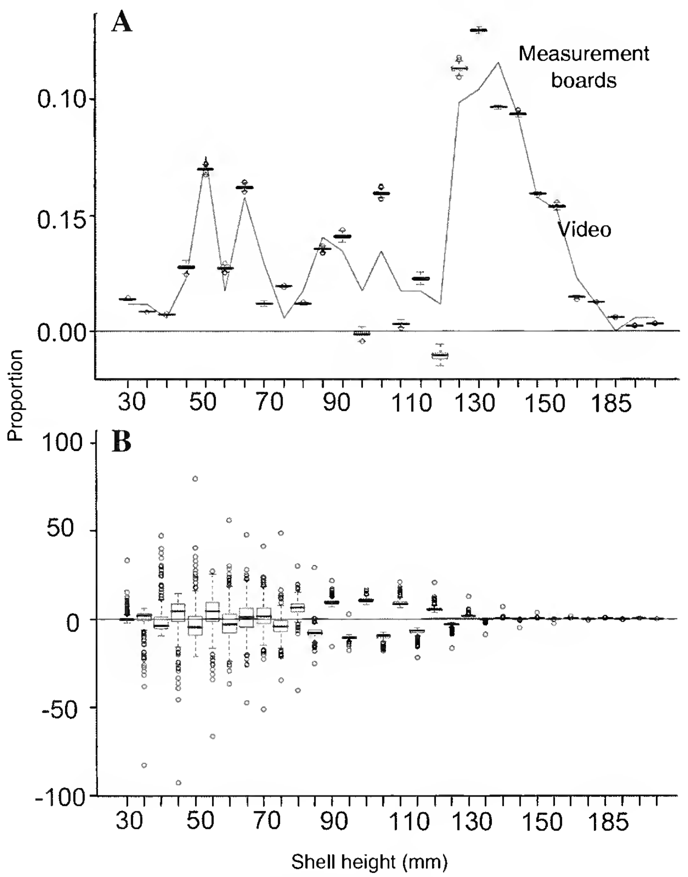
where $\|E\|$ = the matrix norm of E.

The condition factor κ is always at least one and is an upper bound measure of the extent to which errors in the original error matrix E (ignoring errors in $\bar{p}$) will propagate to its inverse. If κ is slightly larger than one, then uncertainty in E^{-1} and $\hat{\bar{\pi}}$ from Equation A4 will be at most slightly greater then uncertainty in E. If κ is large, then uncertainty in E^{-1} and $\hat{\bar{\pi}}$ may be much larger than uncertainty in E.

The measurement-error matrices that included both bias and imprecision are the most realistic according to results from experiment 2. The condition factors for these error matrices were 2638 for video and 2.3 for measuring boards (Table 4). These condition factors indicate that uncertainty in E^{-1} and "corrected" shell-height composition data could be much higher than uncertainty in the original error matrix E for video and at most 2.3 times higher for measuring boards.

Bootstrap analyses show the practical significance of condition factors for video and measuring board data in our study. For example, for the video shell-height measurements in experiment 2, the first step was to resample n data records (including one video measurement and the corresponding caliper measurement) with replacement from the data in experiment 2.

Sample sizes (n=670 for video and n=344 for measuring boards) were the same as the number of experimental measurements and constituted an upper bound on the true effective sample size because they ignore repeated measurements on the same specimens (Table 2). The effect of using an upper bound estimate for effective sample size was to understate effects of uncertainty in error matrices. Our interest was, however, in a "best case" scenario with relatively large sample sizes. Next, the measurement errors (e.g. video or measuring board minus caliper measure-



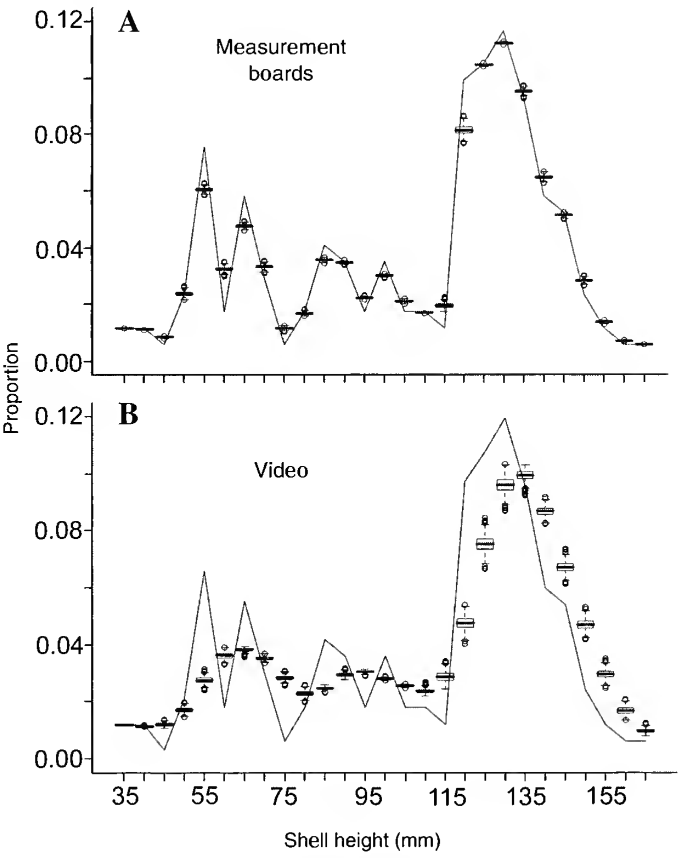
Appendix Figure 1

Boxplots showing bootstrap distributions (1000 iterations) of estimated true shell-height (SH) composition for Atlantic sea scallops (*Placopecten magellanicus*) in experiment 2, based on measurement boards (**A**) and video (**B**) shell-height data. True shell-height compositions were estimated by using bootstrap estimates of the inverse of the measurement error matrix E and Equation A4. The solid line in (**A**) shows the actual caliper-derived shell-height data in the experiment. The solid line is not visible in (**B**) because of the scale of the y-axis.

ments), their mean (bias), and variance were used to calculate the bootstrap measurement error matrix and its inverse. Finally, the original video shell-height composition data used in experiment 2 (expressed as proportions) were then multiplied by the bootstrap inverse matrix (Eq. A4) to remove measurement errors and obtain a bootstrap estimate of the true shell-height composition. There were 1000 bootstrap iterations for both the video and measurement board data. The variability among bootstrap estimates of the true shell-height composition was due entirely to errors in the measurement error matrix E and its inverse E^{-1}.

As expected, based on condition factors (see above) and measurement error statistics (Table 2), bootstrap estimates of true caliper shell-height composition data from video data were highly variable and predicted proportions ranged from −188 to 195 (i.e., outside the feasible range for proportions). Bootstrap estimates from measurement board data resembled the corresponding true caliper measurements. However, the estimated proportions for both measurement methods were often negative and infeasible (Appdx. Fig. 1).

We used a similar bootstrap procedure to evaluate effects of uncertainty in predicted length compositions with measurement errors (Eq. A3 in Appdx. 1), which is the approach used in the CASA model. In this bootstrap analysis, the caliper shell height composition data from experiment 2 were assumed to be true and error matrices were generated by bootstrapping the experimental and video and measuring board data as described above. The sample size was n=172 for both video and measuring boards and the same as the number of individual specimens in experiment 2. This lower bound estimate of the effective sample size was used in order to overstate effects of uncertainty in error matrices. Results indicated that the calculations used in the CASA model for measurement errors were robust to uncertainty about the error matrices and the magnitude of the errors because variability in predicted shell height compositions was relatively minor (Appdx. Fig. 2).



Appendix Figure 2

Bootstrap distributions (1000 iterations) for Atlantic sea scallop (*Placopecten magellanicus*) shell-height data obtained from measurement boards (**A**) and video (**B**), with measurement errors. The solid line shows the actual caliper-derived shell-height data in experiment 2.

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