

Abstract—The hypothesis that heavy fishing pressure has led to changes in the biological characteristics of the estuary cobbler (*Cnidoglanis macrocephalus*) was tested in a large seasonally open estuary in southwestern Australia, where this species completes its life cycle and is the most valuable commercial fish species. Comparisons were made between seasonal data collected for this plotsid (eltail catfish) in Wilson Inlet during 2005–08 and those recorded with the same fishery-independent sampling regime during 1987–89. These comparisons show that the proportions of larger and older individuals and the catch rates in the more recent period were far lower, i.e., they constituted reductions of 40% for fish ≥ 430 mm total length, 62% for fish ≥ 4 years of age, and 80% for catch rate. In addition, total mortality and fishing-induced mortality estimates increased by factors of ~2 and 2.5, respectively. The indications that the abundance and proportion of older *C. macrocephalus* declined between the two periods are consistent with the perception of long-term commercial fishermen and their shift toward using a smaller maximum gill net mesh to target this species. The sustained heavy fishing pressure on *C. macrocephalus* between 1987–89 and 2005–08 was accompanied by a marked reduction in length and age at maturity of this species. The shift in probabilistic maturation reaction norms toward smaller fish in 2005–08 and the lack of a conspicuous change in growth between the two periods indicate that the maturity changes were related to fishery-induced evolution rather than to compensatory responses to reduced fish densities.

Manuscript submitted 5 September 2010.
Manuscript accepted 4 March 2011.
Fish. Bull. 109:247–260 (2011).

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

Changes in catch rates and length and age at maturity, but not growth, of an estuarine plotsid (*Cnidoglanis macrocephalus*) after heavy fishing

Benjamin M. Chuwen (contact author)¹

Ian C. Potter¹

Norman G. Hall¹

Steeg D. Hoeksema¹

Laurie J. B. Laurenson²

Email address for contact author: b.chuwen@murdoch.edu.au

¹ Centre for Fish and Fisheries Research
School of Biological Sciences and Biotechnology
Murdoch University, South Street
Murdoch, Western Australia 6150, Australia

² School of Life and Environmental Sciences
Deakin University
Princes Highway
Warrnambool, Victoria 3280, Australia

The intense harvesting of a fish stock can be accompanied by changes in certain life history traits of that stock. For example, after heavy exploitation, Atlantic cod (*Gadus morhua*) in the northwestern Atlantic and haddock (*Melanogrammus aeglefinus*) on the Scotian Shelf matured at smaller sizes and younger ages (Olsen et al., 2004, 2005; Neuheimer and Taggart, 2010). Because earlier maturing individuals are more likely to reproduce before capture than late maturing individuals, such changes could have been the result of selection for the genotype for maturation at a smaller size or younger age (Marshall and Browman, 2007). It is relevant, however, that the results of simulation studies indicated that, although the harvesting of both immature and mature individuals and also only immature individuals of a stock leads to selection for a reduction in length and age at maturity, the restriction of harvesting to only mature individuals produces the reverse effect (Law and Grey, 1989; Heino, 1998; Ernande et al., 2004).

Laboratory studies have shown that extreme selective harvesting of the largest individuals of Atlantic silverside (*Menidia menidia*) over four generations led to a reduction in growth rate (Conover and Munch,

2002) and that this trend was reversed over five generations when harvesting was relaxed (Conover et al., 2009). The above reduction in growth was attributed to the selection of individuals with genotypes for slower growth, whereas the subsequent increase in growth was related to the removal of those strong selection pressures. Although the above experiments are important in that they reveal that selection can lead to changes in growth, such researchers as Hilborn and Minte-Vera (2008) and Brown et al. (2008) considered that they introduced more extreme selection pressures in their experiments than are likely to be encountered by wild populations and did not take into account the type of density-dependent effects that might be experienced by such populations. On the basis of a meta-analysis of 73 commercially fished stocks of marine species, Hilborn and Minte-Vera (2008) concluded that there was no conspicuous overall trend for growth to either increase or decrease in relation to fishing intensity. Furthermore, their simulation studies indicated that the selectivity patterns of most commercial fisheries would be unlikely to result in substantial evolutionary changes in growth.

The results of several studies indicate that the growth of certain species can alter in response to changes in their density. For example, the growth of porbeagle (*Lamna nasus*) increased following a marked decline in the abundance of this species due to heavy exploitation (Cassoff et al., 2007) and, on the basis of data for eight populations, the growth of immature walleye (*Sander vitreus*) was estimated to have increased 1.3 times when abundance was low rather than high (Venturelli et al., 2010). Furthermore, the growth of Atlantic herring (*Clupea harengus*) on the Georges Bank in the northwestern Atlantic decreased when the abundance of that stock rose after the collapse of that fishery (Melvin and Stephenson, 2007). Although these authors concluded that such changes in growth were related to changes in density, such density-dependent phenotypic expressions are likely to occur only when there is strong competition for a limited supply of food or other essential resources (Brander, 2007).

Maturation reaction norms, which describe the probability that a fish will mature as a function of its length and age, have been used to assess whether changes in the length and age at maturation of some species are likely to be due to genotypic or phenotypic influences, or both (Stearns and Koella, 1986; Heino et al., 2002a, 2002b; Dieckmann and Heino, 2007). For example, this approach has shown that the maturation reaction norm for European plaice (*Pleuronectes platessa*) shifted toward younger ages and smaller lengths with intensive exploitation, indicating that short-term phenotypic responses were overlaid by a longer-term genetic response (Grift et al., 2003).

In none of the previous studies had the question of whether the biological characteristics of a stock of a species have changed in response to fishing pressure been investigated by using fishery-independent data for a heavily fished species whose life cycle is confined to an estuary. The estuary cobbler (*Cnidoglanis macrocephalus*), which is endemic to southern Australia and represented by discrete populations in estuaries (Laurenson et al., 1993a; Ayvazian et al., 1994), is the greatest contributor to the overall value of the commercial estuarine fishery on the south coast of Western Australia (Smith and Brown¹) and is a major component of the ichthyofaunal communities of seasonally open estuaries in this region (Chuwen et al., 2009a). The vast majority of the catch of this benthic plotsid is taken in Wilson Inlet, and long-term, experienced commercial fishermen have become increasingly concerned that the abundance of large *C. macrocephalus* has declined during recent years (McIntosh²; Miller³).

The collection of sound biological data for *C. macrocephalus* in Wilson Inlet in 1987–89 (Laurenson et al., 1993a, 1993b, 1994) provided an excellent opportunity to replicate that fishery-independent sampling regime in 2005–08, and thus elucidate whether the biological characteristics of this plotsid have changed in a manner that would be consistent with continued heavy exploitation. Because individuals of the population of *C. macrocephalus* complete their entire life cycle within Wilson Inlet, we had the particular advantage of sampling the full distribution of that population. Initial comparisons between the fishery-independent data for 1987–89 and 2005–08 confirmed the opinion of commercial fishermen that the prevalence of larger (and thus probably older) *C. macrocephalus* and the abundance (catch rate) of this species declined between the two periods. These comparisons also revealed that the decline in abundance of *C. macrocephalus* in Wilson Inlet was matched by, and consistent with, a corresponding increase in fishing mortality. In view of these findings, focus was subsequently placed on elucidating 1) whether the increased and heavy exploitation of *C. macrocephalus* in Wilson Inlet was accompanied by a reduction in the length and age at maturity; and 2) whether growth changed between the two periods. Reaction norms relating the probability of maturation to length and age were examined to elucidate whether these norms changed in a way that would be consistent with genetic rather than phenotypic changes.

Materials and methods

Sampling regime

Cnidoglanis macrocephalus was sampled in each season between winter 2005 and autumn 2008 at the same six sites in the Wilson Inlet basin that were sampled between winter 1987 and autumn 1989 (Laurenson et al., 1993a, 1993b, 1994). These sites included two that were in the small region closed to commercial fishing and four that were open to such fishing (Fig. 1). The data derived from these samples were used to compare the catch rates and mortality during the two periods. Additional samples were collected from other sites (Fig. 1) to augment the numbers used for determining the length and age at maturity and growth. Note that, to ensure comparability between periods, the raw fishery-independent data obtained during 1987–89 were used to estimate the catch rates, mortality, length and age at maturity, and growth of *C. macrocephalus* in that period in precisely the same manner as that employed for the corresponding data collected during 2005–08.

At each site during 2005–08, nearshore, shallow waters of Wilson Inlet were sampled with a seine net, and

¹ Smith, K., and J. Brown. 2008. South coast estuarine managed fishery status report. In State of the fisheries report 2007/08 (W. J. Fletcher and K. Santoro, eds.), p. 216–223. Dept. Fisheries, Perth, Western Australia.

² McIntosh, O. 2009. Personal commun. Commercial fisherman, Crusoe Beach Road, Denmark, Western Australia, 6333.

³ Miller, W. 2009. Personal commun. Commercial fisherman, Crusoe Beach Road, Denmark, Western Australia, 6333.

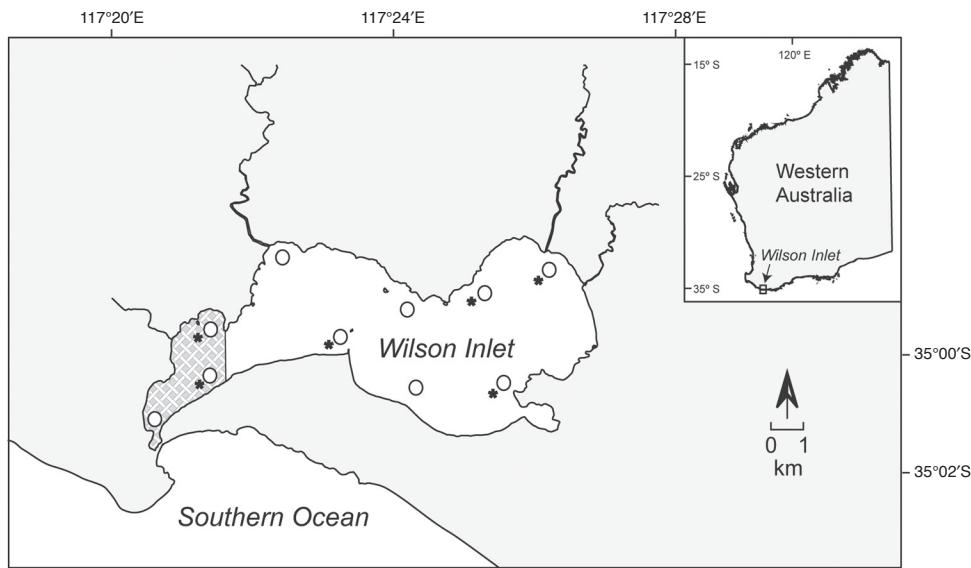


Figure 1

Map showing the location of Wilson Inlet on the south coast of Western Australia and the ten sites sampled for estuary cobbler (*Cnidoglanis macrocephalus*) during 2005–08 (○) and the six also sampled in 1987–89 (*). Hatching represents the area closed to commercial fishing.

offshore, deeper waters were sampled with gill nets and traps baited with the river prawn *Macrobrachium idae*. The seine net, which was 21.5-m long and consisted of two 10-m long wings (6 m of 9-mm mesh and 4 m of 3-mm mesh) and a 1.5-m bunt of 3-mm mesh, was laid parallel to the shore and then hauled on to the beach. This net fished to a depth of 1.5 m and swept an area of ~116 m². The sunken composite multifilament gill net comprised six 20-m panels, each with a height of 2 m, but containing a different stretched mesh size, i.e., 35, 51, 63, 76, 89, or 102 mm. The traps were 500×250×250 mm and contained two funnel entrances 50 mm in diameter. Gill nets and traps were set at dusk and retrieved ~12 hours later around dawn. Fishes were euthanized in an ice slurry immediately after capture. Seasonal values for salinity, water temperature, and dissolved oxygen concentration in Wilson Inlet are given in Chuwen et al. (2009b).

Catch rates

The catch rate for *C. macrocephalus* at each site on each sampling occasion during 1987–89 and 2005–08 was expressed as the number of fish caught overnight (~12 h) in a gill net comprising six panels that were of the same length (20 m) but different mesh sizes (see above). Because spawning peaks in December, thus leading to the recruitment of the new year class in January, comparisons between the catch rates in the earlier and later periods were restricted to using the samples collected seasonally between the summer and spring of 1988, 2006, and 2007, years in which data were obtained at the same sites in open and closed fishing waters in each season (Fig. 1). Analysis of variance (ANOVA) was used

to determine whether the catch rates with gill nets in Wilson Inlet were significantly related to year, season, and region (open vs closed waters), each of which were considered fixed factors. Before analysis, catch rates were fourth-root transformed, which was shown to be appropriate from the relationship between the \log_{10} of the standard deviation and the \log_{10} of the mean catch rates of the replicate samples obtained seasonally from each region in each year.⁴ The catch rates, derived from data collected in the winter and spring of 1987 and the summer and autumn of 1989, were then compared with those for the corresponding seasons during 2005–08 to ascertain whether the results obtained for these more restricted periods paralleled those based on seasonal data for full years. Mean catch rates and 95% confidence limits (CL) were back-transformed before being plotted or reported.

Age determination

The total length (TL) of each *C. macrocephalus* was measured to the nearest 1 mm and its two lapillus otoliths were removed, cleaned, dried, and stored. One otolith from each fish was placed in a black dish, covered with methyl salicylate, and its clearly defined translucent zones were counted under reflected light with a dissecting microscope. Previous work by Laurenson et al. (1994) had validated that a single translucent zone is laid down annually in the lapillus otoliths of *C. macrocephalus*. The age of each fish was estimated by the number of trans-

⁴ Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd ed., 172 p. PRIMER-E, Plymouth, UK.

lucent zones in its otolith, the date when newly formed translucent zones typically become delineated from the otolith periphery, i.e., December–January (Laurenson et al., 1994), the date of capture of the fish, and the birth date, represented by the peak date of spawning, i.e., 1 December (Laurenson et al., 1993a).

Gillnet selectivity and mortality

Gillnet mesh selectivity values for *C. macrocephalus*, which were required to eliminate possible selection bias in research samples of age composition, were calculated for the composite gill net by using the method and model described by Kirkwood and Walker (1986). The function describing selectivity for fish of different lengths by gillnet panels with different mesh sizes is determined by fitting gamma distributions to the length compositions of fish caught in each of the range of different mesh sizes in the gill net. The means of the gamma distributions are assumed to have a linear relationship with mesh size.

The probability distribution function of a variable x that has a gamma distribution is

$$\{x^\alpha \exp(-x/\beta)/\Gamma(\alpha+1)\}/\beta^{\alpha+1},$$

where α and β are the parameters of this distribution. The mode of the distribution is at $x=\alpha\beta$, and the variance is $(\alpha+1)\beta^2$. Kirkwood and Walker (1986) define θ_1 as the constant of proportionality between the modal length and mesh size m , i.e., $\alpha\beta=\theta_1 m$, and assume that the variance of the distribution is constant over the different mesh sizes, denoting this by θ_2 . By relating this variance to the equation for the variance of the gamma distribution, Kirkwood and Walker (1986) advise that

$$\beta = -0.5 \left\{ \theta_1 m - (\theta_1^2 m^2 + 4\theta_2)^{0.5} \right\}.$$

The fishing-induced mortality (F) of fully vulnerable fish was estimated by using the age composition data derived from gillnet sampling in 1988 and 1989 and in 2006, 2007, and 2008. The model used for this analysis, which is described in detail below, was based on the relative abundance model described by Deriso et al. (1985). Because mature males of *C. macrocephalus* excavate burrows before the spawning period and protect their small juveniles within those burrows, the data used to estimate F were restricted to those collected in late summer (February) and autumn (May) to eliminate the possible effects of such behavior on the age composition of this population. For this model a constant known level of natural mortality (M) is assumed, i.e., the value for the estimate calculated from the maximum age recorded for *C. macrocephalus* by employing Hoenig's (1983) equation for natural fish mortality.

It was assumed that fish longer than the minimum legal length (MLL) for retention (i.e., 430 mm TL) are fully exposed to a constant level of fishing mortality,

whereas those that were shorter than the MLL experience no fishing mortality and are affected only by natural mortality. Thus, the age composition of the population within the estuary will reflect this pattern of fishing mortality. However, the age composition of the population was assumed to be influenced not only by natural and fishing mortality, but also by interannual variability in recruitment strength. Thus, the number of fish of age a and year class y in year t may be assumed to be represented by

$$N_{a,y,t} = \begin{cases} R_y & \text{if } a = a_1 \\ R_y \exp \left[-\sum_{j=a_1}^{a-1} Z_j \right] & \text{if } a > a_1 \end{cases}, \quad (1)$$

where R_y = the annual recruitment (to age a_1) for year class y (where $y=t-a$);

a_1 = the first age present in the age-composition data; and

$Z_a = M + F_a$ = the total mortality experienced by fish of age a .

The fishing mortality of fish of this age is zero if the length of fish at the midpoint of the ages in the age class is less than the MLL, otherwise $F_a = F$, the fishing mortality of fully vulnerable fish. The above equation for $a > a_1$ may be rewritten as

$$N_{a,y,t} = R_y \exp[-M(a-a_1)] \exp \left[-F \sum_{j=a_1}^{a-1} S_j \right], \quad (2)$$

where S_a = the selectivity of the fishing gear used in commercial fishing and it is assumed that $S_a = 0$ if the length of fish at the midpoint of the ages in the age class is less than the MLL, otherwise $S_a = 1$.

Denoting the expected count of fish of age a caught from year class y in year t by $\hat{c}_{a,y,t}$, we may express this as

$$\hat{c}_{a,y,t} = I_t S_a^* N_{a,y,t},$$

where I_t is a factor that represents a combination of the catchability of the fully vulnerable fish and the fishing effort used to collect the research sample in year t , i.e., the sampling intensity in that year, and S_a^* is the selectivity of the research fishing gear used for collecting the age composition data.

Thus,

$$\log_e \hat{c}_{a,y,t} = \log_e I_t + \log_e S_a^* + \log_e R_y - M(a-a_1) - F \sum_{j=a_1}^{a-1} S_j,$$

where the summation term is set to zero if $a=a_1$.

The cumulative sum of the age-dependent selectivities of the commercial fishing gear to which the stock was exposed before age a , i.e., from age a_1 to age $a-1$, may be written as

$$K_a = \sum_{j=a_1}^{a-1} S_j$$

for $a > a_1$ and $K_{a_1} = 0$, and we may express this model as

$$\log_e \hat{c}_{a,y,t} = \log_e I_t + \log_e S_a^* + \log_e R_y - M(a - a_1) - FK_a.$$

If we assume that M , S_a^* , and S_a are known, then the observed counts of fish within the various age classes for each sampling year may be considered to be random variates drawn from Poisson distributions, the means of which may be calculated with the above equation. Thus, with R software (R Development Core Team, 2008), Poisson regression analysis was used to fit the above model to the age-composition data for *C. macrocephalus* collected in each period and thereby to obtain estimates (and standard errors) of both the relative year class strengths and the fishing mortality reflected in those data. Because the sampling intensity employed in the different years was constant, it was removed from the model. Profiles of the residual deviances versus fishing mortality were constructed for each period by fitting the model to a set of fixed values of F over a wide range and by recording the resulting estimate of residual deviance for each value of F . Approximate 95% CLs for F were then selected as those values less than and greater than the maximum likelihood estimate of F and which produced residual deviances different from that at the maximum likelihood estimate by a value equal to $\chi^2_{0.05}(1)$ i.e., 3.84.

Length and age at maturity

The gonads of each fish were identified macroscopically as either ovaries or testes, or as indeterminate in the case of juvenile fish with very small gonads. On the basis of their macroscopic characteristics and the scheme of Laevastu (1965), the gonads of each fish were allocated to one of the following eight stages of gonadal development: I-II=immature or resting adult; III=developing; IV=maturing; V=respawning; VI=spawning; VII=spent; and VIII=recovering spent.

Because gonads at stages I and II could not be distinguished morphologically, we could not use the macroscopic appearance of gonads to differentiate between virgin fish and fish that may have already spawned. However, the trends exhibited by the prevalences of the different gonad stages of fish caught in sequential months before and during the spawning period indicated that the gonads of the larger fish, e.g., greater than the length at which 95% of fish are mature (L_{95}), would almost invariably have been destined to progress through to stage VIII if the fish had survived. This point is substantiated by the fact that the maturity ogives, derived by using gonads at stage III or higher during the spawning period as the indicator that a fish will become or has reached maturity during that period, have asymptotes of 100% (see *Results* section). In other words, during the spawning period, the gonads of any fish remaining in the stage I-II category are

virgin gonads, i.e., stage I. Fish that possessed gonads at stages III–VIII during the spawning period were classified as mature.

In each season, the gonads of up to 20 females, covering a wide range of lengths and the full suite of gonadal stages observed in that season, were retained and prepared for histological examination. For this purpose, a portion of the mid-region of one ovarian lobe was placed in Bouin's fixative for ~48 hours and dehydrated in a series of increasing concentrations of ethanol. The ovarian portions were then embedded in paraffin wax, cut transversely into 6 mm sections and stained with Mallory's trichrome. The stages in oocyte development in each ovarian section were then determined by examination with a Leica MZ7.5 dissecting microscope (Leica Microsystems, Wetzlar, Germany) to validate that each ovary had been assigned to the appropriate stage on the basis of its macroscopic appearance.

The lengths (L_{50} and L_{95}) and ages (A_{50} and A_{95}) at maturity were estimated for the females of *C. macrocephalus* in Wilson Inlet during 2005–08 and, with the raw data of Laurenson et al. (1993a), also for 1987–89. In the case of fish lengths, logistic regression analysis was used to fit curves to the probabilities that female fish at each length during that year's spawning period would possess gonads at one of stages III–VIII and were thus mature or destined to become mature during that spawning period. The logistic equation describing the probability of an individual possessing mature gonads, P , at length, L , was

$$P = \left[1 + \exp(-\log_e(19)(L - L_{50})/(L_{95} - L_{50})) \right]^{-1},$$

where the parameters L_{50} and L_{95} are the total lengths at which 50 and 95% of the individuals, respectively, would be expected to possess gonads at stages III–VIII.

On the basis of its length, the likelihood of the j th fish possessing or not possessing gonads at stages III–VIII was calculated as P_j or $1 - P_j$, respectively. Setting $X_j = 0$ if the j th fish did not possess gonads at such a stage and setting $X_j = 1$ if it did possess such gonads, the overall log-likelihood, λ , was calculated as

$$\sum_j \{ X_j \log_e P_j + (1 - X_j) \log_e [(1 - P_j)] \}.$$

The logistic equation was fitted by maximizing this log-likelihood with SOLVER in Excel (Microsoft Corp., Redmond, WA). The data were randomly resampled and analyzed to create 1000 sets of bootstrap estimates of the parameters of the logistic equation and the probabilities of females and males being mature for each of a range of specified lengths. The 95% CLs of the probability of maturity at each specified length were taken as the 2.5 and 97.5 percentiles of the corresponding predicted values resulting from this resampling analysis. The medians of the bootstrap estimates were used as the point estimates of each parameter and of the probability of maturity at each specified length. The A_{50} for the females of *C. macrocephalus* at maturity were estimated

by the same procedure outlined above, but by substituting ages for lengths.

The logistic regressions describing the lengths and ages at maturity for female *C. macrocephalus* during 2005–08 and 1987–89 were compared by using a likelihood-ratio test (Cerrato, 1990). The log-likelihood, λ , which, ignoring constants, was calculated with SOLVER in Excel as

$$\lambda = -\frac{n}{2} \log_e \frac{ss}{n},$$

where n = sample size; and

ss = the sum of squared residuals between the observed and expected lengths and ages at maturity.

The value of a test statistic, G , was then calculated as twice the difference between the log-likelihoods obtained by fitting a common curve for both periods and that obtained by fitting a separate curve for each period. The hypothesis that the lengths and ages at maturity in the two periods could be described by a single curve was rejected at the $\alpha=0.05$ level of significance if $G>\chi^2_a(q)$, where q is the difference between the numbers of parameters in the two approaches.

Growth

Von Bertalanffy growth curves were fitted to the lengths at age of *C. macrocephalus* at the date of capture for both 1987–89 and 2005–08. The von Bertalanffy growth equation for describing growth is $L_t = L_\infty (1 - e^{(-k(t-t_0))})$, where L_t is the length (mm TL) at age t (years), L_∞ is the asymptotic length (mm TL) predicted by the equation, k is the growth coefficient (per year) and t_0 is the hypothetical age (years) at which fish have zero length. The parameters for the von Bertalanffy growth equation and their 95% CLs were estimated from the lengths at age of fish at the date of capture by employing the nonlinear regression routine in SPSS (IBM Corp., Somers, NY).

The von Bertalanffy growth equations for females and males were compared using the likelihood-ratio test described above. The same likelihood-ratio test was used to compare the growth of *C. macrocephalus* during the current study (2005–08) with that derived for 1987–89 from the raw data collected by Laurenson et al. (1994). Because the likelihood-ratio test identifies very small differences in growth as statistically significant for large sample sizes, emphasis was placed on the level of difference in growth that was likely to be of biological significance. Such differences were considered to exist when any of the predicted lengths at integer ages ≥ 1 year in the range of the dominant ages within the data, i.e., 1 to 4 years, differed by $>5\%$ of the mean of the two asymptotic lengths (see *Results* section).

Maturation reaction norms

Probabilistic reaction norms for length and age at maturation (Heino et al., 2002a; Barot et al., 2004) were

determined for each period. For this purpose, logistic regression analysis was employed to relate the probability that a fish was mature to its length and age, i.e.,

$$P = \left\{ 1 + \exp[-(\alpha + \beta L + \gamma A)] \right\}^{-1}.$$

The logistic regression equations for the two periods were compared by using the likelihood-ratio test. The probability of a fish maturing at age A was then calculated as

$$m(A, L) = [P(A, L) - P(A-1, L-\Delta L)] / [1 - P(A-1, L-\Delta L)],$$

assuming that, if a fish was of length L at age A , then, from the von Bertalanffy curve fitted to the data for the period,

$$L - \Delta L = L \exp(k) - L_\infty [\exp(k) - 1].$$

Note that, in this equation, L is not assumed to be the expected length at age, but represents the length of an individual fish. By setting $m(A, L)$ and solving the equation, the value of L may be estimated for any specified value of A to determine those lengths and ages at which the probability of fish maturing was 50% and conditional on the fish being alive at those ages. The contours represented by these midpoints of the reaction norms for the two periods were plotted and overlaid by the von Bertalanffy growth curves for those periods.

Water temperatures

Because water temperatures can influence maturation or growth (or both) and thus maturation reaction norms (Neuheimer and Taggart, 2007, 2010), the possibility that temperature was greater during either 1987–89 or 2006–08 was explored. Although there were no daily recordings of water temperature for Wilson Inlet during the two periods, such data are available for air temperature at Albany in the vicinity of Wilson Inlet (Australian Bureau of Meteorology: <http://www.bom.gov.au/climate/data/>, accessed November 2010). One-sample t -tests with SPSS software were used to examine whether, for both the minimum and maximum temperatures, the mean of the pairwise differences between the average monthly air temperatures in corresponding months over each of the 120 consecutive months of 1980–1989 and 1998–2007 was significantly different from zero. These periods encompassed all or the vast majority of the thermal history of fish caught during the two sampling periods.

Results

Length and age compositions and catch rates

Although *C. macrocephalus* caught with research gill nets at the same sites in Wilson Inlet during 1987–89 and 2005–08 covered a similar length range, i.e., ~160

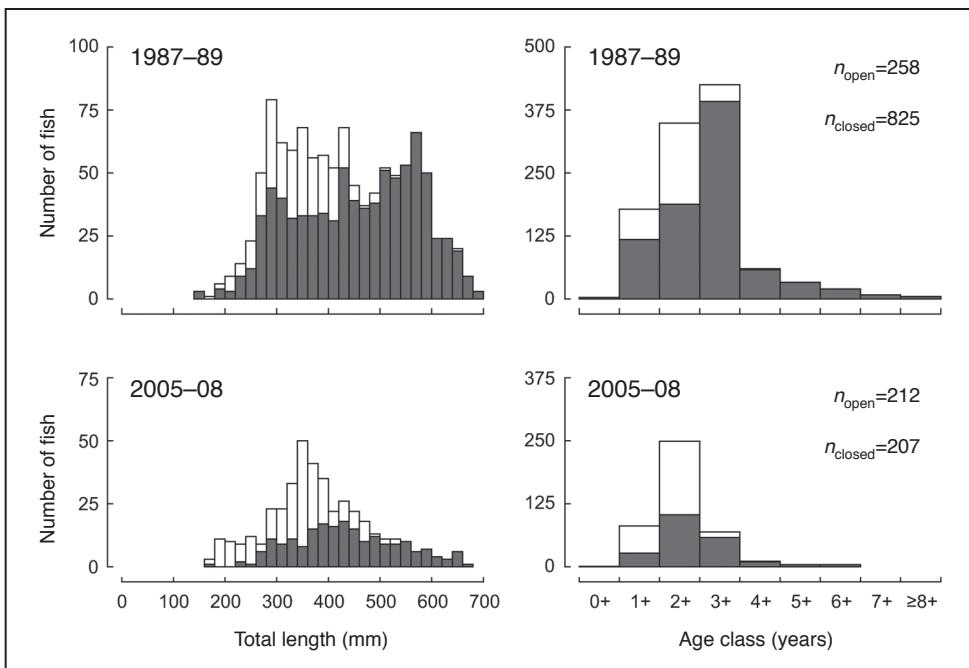


Figure 2

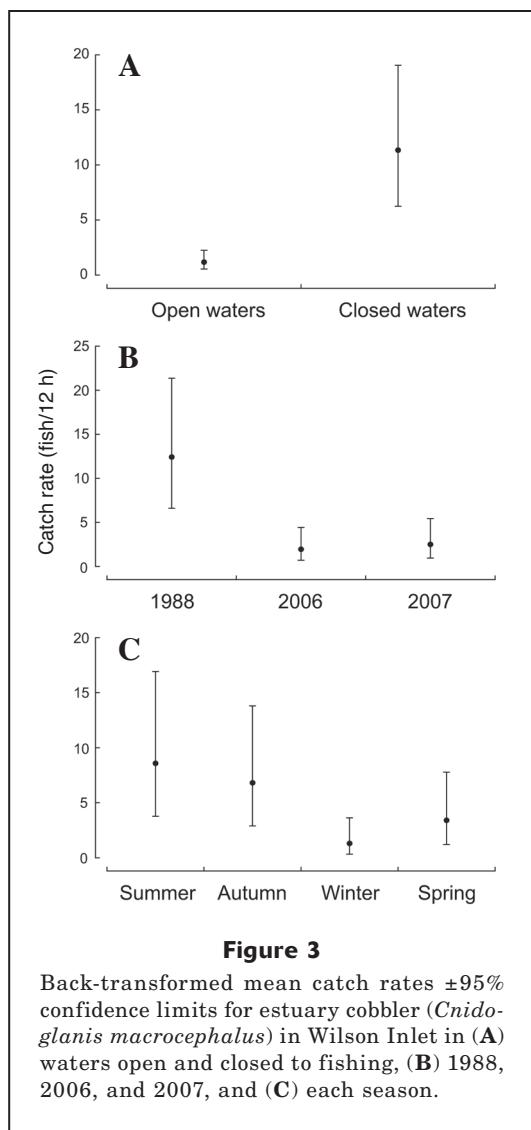
Length- and age-class frequency distributions for estuary cobbler (*Cnidoglanis macrocephalus*) caught with gill nets at the same sites in Wilson Inlet during 1987–89 and 2005–08. Shaded areas represent the number of individuals in each length and age class that were caught in areas closed to commercial fishing. Four sites were sampled in the area open to fishing and two sites were sampled in the closed area during both time periods (1987–89 and 2005–2008). Sample sizes (n) for the number of individuals caught in open versus closed areas are given.

to 700 mm TL, the length-frequency distribution in the earlier period contained a second strong modal length class at 560–579 mm TL, which exceeded the length of the vast majority of fish caught in the later period (Fig. 2). Consequently, the percentage of fish >430 mm TL, the current MLL for retention of this species, was far lower in 2005–08 (29%) than in 1987–89 (48%) (Fig. 2). Although the percentage of fish greater than this MLL in the waters open to commercial fishing were similarly low in both periods (12% in 1987–89 and 10% in 2005–08), the percentage of such fish was less in the area closed to commercial fishing in 2005–08 (48%) than in 1987–89 (60%) (Fig. 2).

Although the 3+ age class of *C. macrocephalus* was the best represented age class in the catches taken with gill nets during 1987–89, closely followed by the 2+ age class, the catches during 2005–08 were dominated by the 2+ age class and contained few age 3+ fish (Fig. 2). The 4+ age class was also reasonably well represented in the earlier but not the later period and the percentage of fish ≥4+ years was 11.7% during 1987–89 compared with 4.5% during 2005–08 (Fig. 2). In both periods, the vast majority of *C. macrocephalus* ≥4+ years were caught in the region closed to commercial fishing (Fig. 2).

Analyses of the catch rates of *C. macrocephalus* in each region of Wilson Inlet, i.e., sites open and closed

to commercial fishing, in each season of 1988, 2006, and 2007, revealed that catch rates were significantly related to region ($P<0.001$), year ($P<0.01$), and season ($P<0.05$), and that none of the interactions between those main effects was significant (all $P>0.05$) (Table 1). The mean catch rate in the area closed to commercial fishing was 11.3 fish/12 h and far greater than in the area open to commercial fishing (1.2 fish/12 h) (Fig. 3A). Although the mean catch rate of *C. macrocephalus* in 2006 (1.9 fish/12 h) did not differ significantly ($P>0.05$) from that in 2007 (2.5 fish/12 h), both catch rates differed significantly (both $P<0.01$) from that in 1988, i.e., 12.4 fish/12 h (Fig. 3B). The mean catch rates of *C. macrocephalus* in Wilson Inlet declined from their maxima in summer and autumn (8.6 and 6.8 fish/12 h, respectively) to their minima in winter (1.3 fish/12 h) and rose again in spring (3.4 fish/12 h) (Fig. 3C). On the basis of the ANOVAs, and recognizing that there was no interaction with either region or season, we determined that the mean catch rates in the winter and spring of 1987 were greater and differed significantly from those in the corresponding seasons of 2005–08 (each $P<0.001$). Mean catch rates were also greater, but not significantly different ($P>0.05$), in four of the six comparisons between the summer and autumn of 1989 and the corresponding seasons of 2005–08.



Gillnet selectivity and mortality

Analyses of the mesh selectivity of the composite gill net for *C. macrocephalus* indicated that stretched meshes of 35, 51, 63, 76, 89, and 102 mm predominantly caught fish with lengths of 160–379, 190–479, 200–549, 270–619, 410–679, and 490–709 mm, respectively (Fig. 4A). The values for θ_1 and θ_2 , derived from the model of Kirkwood and Walker (1986), were 6.1 and 6802, respectively. Trends in estimates of selectivity at age indicated that this species became fully susceptible to capture by the above suite of mesh sizes at ~2 years of age and essentially remained so in the immediately ensuing years (Fig. 4B).

Fishing mortality (F) in Wilson Inlet during 1988–89 was 0.57 per year (95% CL=0.27–0.90 per year) and thus far less than the 1.47 per year (95% CL=1.14–1.84 per year) estimated for the population in this estuary during 2006–08, and there was no overlap of the 95% CLs. Natural mortality (M) of *C. macrocephalus* was calculated to be 0.35 per year on the basis of a maximum age of 14 years (L. J. B. Laurenson, unpubl. data) and thus total mortality (Z) was estimated to be 0.92 per year during 1988–89 and 1.82 per year during 2006–08.

Length and age at maturity

The percent contributions of mature female *C. macrocephalus* to all females in the 400–449 and the 450–499 mm TL length classes during 2005–08 were 62% and 94%, respectively, and thus far greater than the corresponding values of 22% and 67% for 1987–89 (Fig. 5). These differences help account for the L_{50} and L_{95} of females at maturity during 2005–08, i.e., 419 mm TL (95% CL=399–438 mm TL) and 490 mm TL (95% CL=448–538 mm TL), respectively, being significantly different ($P<0.05$) from those during 1987–89, i.e., 449 mm TL (95% CL=434–463 mm TL) and 542 mm TL

Table 1

Mean squares and significance levels for three-way analysis of variance of catch rates of estuary cobbler (*Cnidoglanis macrocephalus*) derived from samples obtained with gill nets in regions open and closed to fishing in Wilson Inlet, Western Australia, in each season of 1988, 2006, and 2007. * $P<0.05$. ** $P<0.01$. *** $P<0.001$.

Main effects				
	Region (R)	Year (Y)	Season (S)	Residual
Degrees of freedom	1	2	3	47
Mean square	9.986***	3.048**	1.312*	0.384
Interactions				
	$R \times Y$	$R \times S$	$Y \times S$	$R \times Y \times S$
Degrees of freedom	2	3	6	6
Mean square	0.720	0.696	0.344	0.831

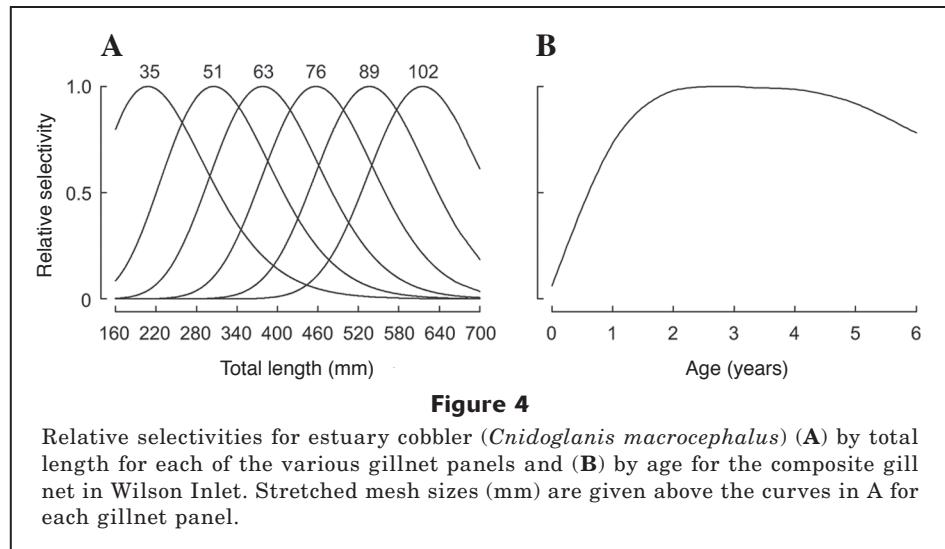


Figure 4

Relative selectivities for estuary cobbler (*Cnidoglanis macrocephalus*) (A) by total length for each of the various gillnet panels and (B) by age for the composite gill net in Wilson Inlet. Stretched mesh sizes (mm) are given above the curves in A for each gillnet panel.

(95% CL=514–569 mm TL), respectively. The percentage of females that were mature at the end of their third year of life was far greater in 2005–08 (62%) than during 1987–89 (15%) and the same was true for females at the end of their fourth year of life (95% vs 73%) (Fig. 5). Consequently, the estimates of the A_{50} and A_{95} for female *C. macrocephalus* at maturity during 2005–08, i.e., 2.9 years (95% CL=2.6–3.1 years) and 3.9 years (95% CL=3.7–4.4 years), were significantly different ($P<0.001$) from those during 1987–89, i.e., 3.5 years (95% CL=3.4–3.7 years) and 4.7 years (95% CL=4.6–5.2 years).

The number of large males caught during the spawning period was very low because, at this time, they tend to occupy burrows within which they brood eggs and rear yolk-sac larvae under their pelvic fins (Laurerison et al., 1993a). It was thus not possible to derive reliable estimates for the L_{50} or A_{50} for the males of *C. macrocephalus*.

Growth

Although the likelihood-ratio test showed that the von Bertalanffy growth curves for females and males of *C. macrocephalus* in Wilson Inlet were significantly different at the $\alpha=0.05$ level of significance (each $P<0.001$) for both 1987–89 and 2005–08, the differences in the estimated lengths at each integer age between 1 and 4 years, ages that encompassed the majority of the data, were less than 3% of the mean of the asymptotic lengths of the two growth curves for each period. The differences were thus considered not to be of biological significance. The length-at-age data for the two sexes in each period were therefore pooled. The von Bertalanffy growth curve provided a good fit to the lengths at age for all but the older *C. macrocephalus* for both 1987–89 and 2005–08; the lengths at age of the relatively small number of older fish were overestimated by the curve (Fig. 6, Table 2).

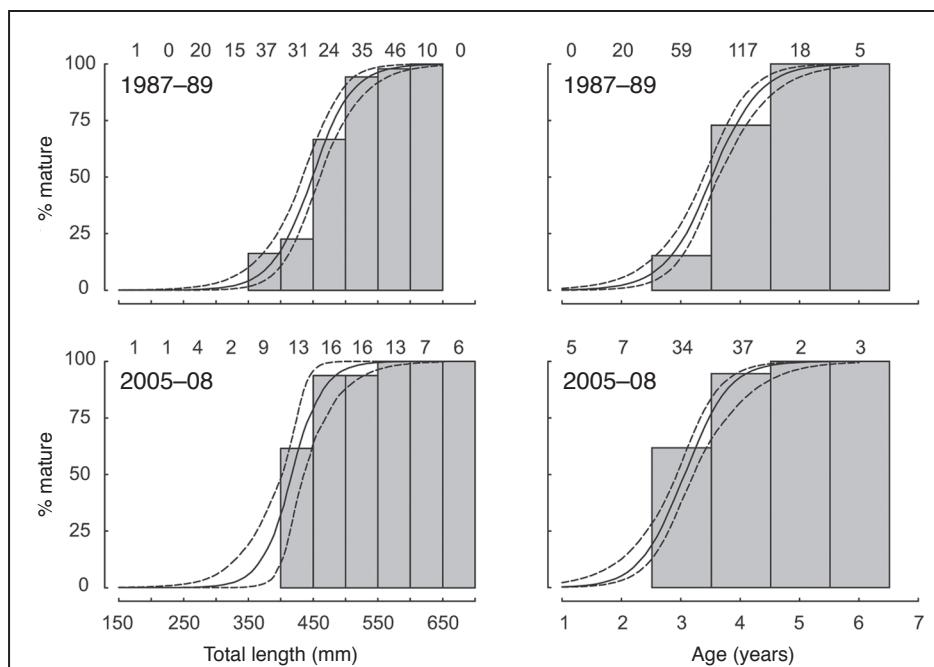
The likelihood-ratio test showed that the von Bertalanffy growth curve for *C. macrocephalus* in Wilson Inlet during 2005–08 differed significantly ($P<0.001$) from the corresponding curve derived for this species for 1987–89 (Fig. 6). However, because the differences in the estimated lengths at each integer age between ages 1 and 4 years (ages that encompassed the majority of fish) were less than 2% of the mean of the two asymptotic lengths, those differences were not considered biologically significant.

Maturation reaction norms

Logistic regression analyses demonstrated that, for both 1987–89 and 2005–08, maturity was better described as a function of length (log-likelihood [LL] = -61.2 and -21.0, respectively) than of age (LL =-102.2 and -31.2, respectively). Furthermore, the quality of the fit was not improved significantly by including age as well as length in the model (both $P>0.05$, LL =-61.2 and -20.0, respectively). Although the coefficient of the length term in the logistic curves relating the probability that a fish was mature to its length and age, i.e., β , differed significantly between the two periods ($P<0.05$), the values for the other parameters (α and γ) did not differ greatly (both $P>0.05$).

As expected, given the lack of significance of age when fitting the logistic regression equation to the combination of both length and age data, each of the reaction norms was essentially independent of age (Fig. 6). In other words, in each period, fish became mature at approximately the same length in that period regardless of their age.

The reaction norm for maturation shifted markedly toward lower lengths at age between 1987–89 and 2005–08, but the slopes of the curves did not change (Fig. 6). The von Bertalanffy growth curves did not differ in biological terms between the two periods, but because the intersection of the growth curves occurred

**Figure 5**

Percent frequencies of occurrence of mature females (ovaries at one of stages III to VIII) in sequential 50-mm total length classes and sequential age classes of estuary cobbler (*Cnidoglanis macrocephalus*) during the spawning period of this species. Logistic curves (solid lines) and their 95% confidence limits (dotted lines) were derived from logistic regression analyses of the relationship between total length and the probability that an individual fish was mature. Sample sizes for each length and age class are shown above each length and age class.

Table 2

Von Bertalanffy growth parameters and their 95% confidence limits (CL) derived from lengths at age of estuary cobbler (*Cnidoglanis macrocephalus*) caught in Wilson Inlet, Western Australia, during 1987–89 and 2005–08. L_{∞} =asymptotic length (mm); k =growth coefficient (per year); t_0 =hypothetical age at which fish would have zero length (yr); r^2 =coefficient of determination; n =sample sizes; L_{max} =maximum lengths (mm); W_{max} =maximum weights (g); and A_{max} =maximum ages (yr).

Von Bertalanffy parameters								
	n	L_{max}	W_{max}	A_{max}	L_{∞}	k	t_0	r^2
1987–89	1301	722	2188	13	831	0.24	-0.09	0.86
					797	0.22	-0.16	
					864	0.26	-0.02	
2005–08	758	712	2576	8	911	0.21	-0.22	0.90
					839	0.18	-0.30	
					982	0.24	-0.14	

at different lengths and ages, the maturation at a smaller size in the later period was accompanied by a reduction in the age at maturity (Fig. 6).

Water temperatures

The mean of the pairwise differences between the average monthly air temperatures in corresponding months

over each of the 120 consecutive months of the two periods did not differ significantly from zero (both $P>0.05$) for either the minimum or maximum temperature. In other words, the air temperatures were not consistently greater in one period than the other. Because Wilson Inlet is shallow, the trends exhibited by these air temperatures will be reflected closely by the water temperatures of this estuary.

Discussion

The fishery in Wilson Inlet is a multisector, i.e., commercial and, to a lesser degree, recreational, multigear, and multispecies fishery, of which the benthic *C. macrocephalus* is just one of several species targeted during commercial fishing. The data recorded by commercial fishermen for the managers of this fishery are greatly influenced by the variable extent to which the different species are targeted overall and during different periods and do not identify the fishing effort directed toward any single species. Such fishery-dependent data thus provide little information on the status of the *C. macrocephalus* stock in Wilson Inlet and how it might be changing over time. At present, such information can only be obtained from the type of fishery-independent data that were collected during the present study. The confinement of the stock of *C. macrocephalus* in Wilson Inlet to that estuary, and the availability of sound biological data for this stock in the 1980s, have provided a particularly good opportunity to explore the effects of heavy fishing on the biological characteristics of an exploited fish population. In particular, the existence of these earlier biological data allowed us to investigate the possibility that length or age at maturity, or both, changed as a result of fishing-induced evolution.

The fact that the mean catch rates of *C. macrocephalus* in Wilson Inlet during 2006–07 were 80–85% less than those in 1988 indicates that the abundance of this plotosid in this estuary declined markedly between those two periods. It is thus highly relevant that the samples during 1987–89 were dominated by age 3+ and to a lesser extent age 2+ fish and contained appreciable numbers of fish ≥4 years old and some ≥7 years old, whereas those in 2005–08 were dominated by the 2+ age class and contained very few fish older than 3 years. The smaller proportion of older fish during 2005–08 is reflected in the smaller percentage of fish caught with lengths greater than the current MLL of 430 mm TL during this more recent period, i.e., 29% vs 48%. The conclusion, based on fishery-independent data, that the numbers of large fish have declined during the last two decades, is consistent with experienced, long-term commercial fishermen responding to a reduction in their catches of larger fish by using a smaller mesh in their gill nets (McIntosh²; Miller³). Because the decline in catch rates between 1987–89 and 2005–08 was related to the marked reduction in the proportion of *C. macrocephalus* with lengths greater than the MLL for retention of this species, there is very strong circumstantial support for the conclusion that this decline was related to the effects of fishing rather than to a change in the environment.

The decline in the relative abundance of larger and older fish in Wilson Inlet between the two periods accounts for the estimates of total mortality, Z , increasing markedly from 0.92 per year during 1987–88 to 1.82 per year in 2006–08. Furthermore, fishing mortality, F , increased from 0.57 to 1.47 per year between those two periods, which represented an

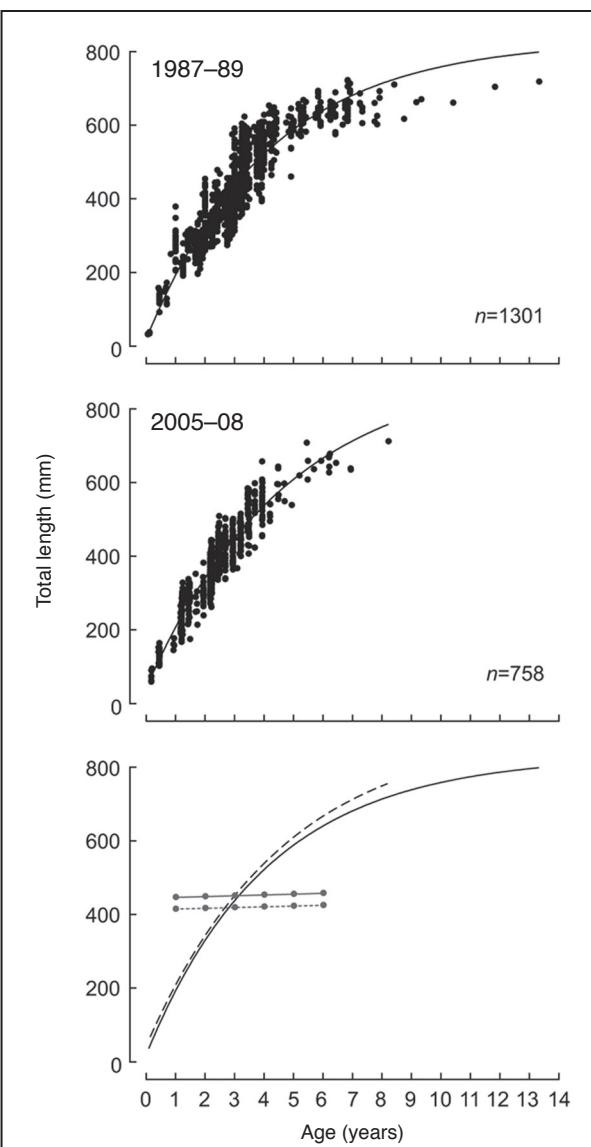


Figure 6
Von Bertalanffy growth curves fitted to lengths at age of estuary cobbler (*Cnidoglanis macrocephalus*) caught in Wilson Inlet during 1987–89 and 2005–08 and a comparison of the curves for 1987–89 (solid line) and 2005–08 (dashed line), which are overlaid with probabilistic maturation reaction norm midpoints (gray) for females at integer ages of 1–6 years.
 n =sample sizes.

increase of more than 250%. Although F in the earlier period was already about 1.6 times that of natural mortality, M , it had become more than four times greater than that of M by 2006–08. The current level of F for this species in Wilson Inlet is therefore well in excess of 0.75 or 0.8 M , which have been considered target reference points for F in data-poor fisheries (Gabriel and Mace, 1999), and is thus at a level unlikely to sustain the fishery. The view that commercial fishing has led

to heavy exploitation of *C. macrocephalus* during the last two decades is supported by the observation that, although fishery-independent catch rates have fallen, the commercial catches of this species in Wilson Inlet have shown no clear tendency to decline between these two periods.¹ This finding emphasizes the difficulties in obtaining reliable values for the catch per unit of effort of a species by using fishery-dependent data for the multispecies fishery of which that species is just one contributor.

A comparison of the age-frequency data for open and closed areas indicated that the relatively small area that is closed to commercial fishing in Wilson Inlet provides some protection for the stock of *C. macrocephalus* in that estuary. Thus, although the catches in open waters contained appreciable numbers of age 1+ and 2+ *C. macrocephalus*, they yielded few age 3+ fish, whereas those in closed waters contained large numbers of 3+ individuals, the age at which this species attains, on average, the MLL of 430 mm TL for retention in the fishery. Furthermore, the catch rates, and thus relative abundances, were greater in closed than open waters.

The MLL for *C. macrocephalus* during 1987–89 was 318 mm TL, and thus considerably less than the L_{50} of 449 mm TL for females at maturity in that period. Therefore, at that time, both mature and immature individuals would have been heavily harvested, leading to selection pressures for a reduction in the length at maturity (Law and Grey, 1989; Heino, 1998; Ernande et al., 2004). Although the MLL was increased to 430 mm TL in 1994, it is reasonable to suggest that substantial numbers of both immature and mature individuals continued to be fished, which would account for selection having led to a reduction in the L_{50} of females at maturity to 419 mm TL during 2005–08.

Comparisons between the reproductive data for *C. macrocephalus* in Wilson Inlet during the two sampling periods indicated that the females of this species matured at a smaller size and younger age during 2005–08 than during 1987–89, with respective L_{50} s of 419 and 449 mm TL and A_{50} s of 2.9 and 3.5 years. The corresponding downward shift of the reaction norms for maturation and the attainment of sexual maturity at smaller sizes and younger ages by the heavily fished *C. macrocephalus* parallel the trends exhibited by the reproductive parameters for populations of several fish species that were also heavily exploited by commercial fishing (e.g., Trippel, 1995; Olsen et al., 2004; Morita and Fukuwaka, 2007; Neuheimer and Taggart, 2010). They also parallel the patterns exhibited by natural populations of guppies (*Poecilia reticulata*) that were subjected to either high or low predation, which thus served as surrogates for the presence or absence of commercial fishing (Reznick and Ghalambor, 2005). A reduction in the size and age at maturity of heavily fished stocks may reflect an increased selection for rapidly maturing individuals because these would be more likely to reproduce before being captured (Marshall and Brownman, 2007). Indeed, Olsen et al. (2005)

provided evidence that the trend for earlier maturation in stocks of the heavily exploited Atlantic cod (*Gadus morhua*) halted and even showed signs of reversing after the fisheries for those stocks had been closed. The shift of the maturation reaction norms toward lower lengths indicates that there has been a genetic response of the stock of *C. macrocephalus* to the intensive exploitation to which it has been shown to have been subjected.

Although the total mortality of *C. macrocephalus* in Wilson Inlet essentially doubled between 1988–89 and 2006–08, the differences between the predicted lengths at age of fish at each of the dominant integer ages in the two periods were <2% and thus considered not to be of biological significance. This absence of a shift in growth after heavy fishing pressure is consistent with the conclusions from a meta-analysis of 73 commercially fished marine stocks that there was no evidence in general, that growth rate was related to fishing intensity (Hilborn and Minte-Vera, 2008). The lack of a clear change in growth after heavy exploitation contrasts with the situation recorded for a number of species in which growth was found to change with heavy exploitation (e.g., Cassoff et al., 2007; Melvin and Stephenson, 2007; Swain et al., 2007). Such changes have generally been attributed either to fishery-induced evolution or density-dependent effects.

Evolutionary effects would account for the reduction in growth that has been recorded for a number of heavily exploited fish populations through size-selective harvest of individuals with the genotype for fast growth (e.g., Jørgensen et al., 2007; Swain et al., 2007; Brown et al., 2008). The density-dependent alternative cause would account for the increased growth that occurs in some fish populations following heavy exploitation and which is considered to represent a compensatory response to the decline in density brought about by the removal of a large number of individuals and thus a reduction in competition for resources (e.g., Trippel, 1995; Cassoff et al., 2007). Because the marked decline in fish density of *C. macrocephalus* in Wilson Inlet between 1987–89 and 2005–08 was not accompanied by an increase in growth, this species did not undergo a density-dependent phenotypic response between the two periods. This finding, in conjunction with the change in the maturation reaction norms, supports our conclusion that the changes in the length and age at maturity of *C. macrocephalus* over time probably represent a genotypic response to fishing pressure.

Conclusions

This study provides further strong indications that heavy fishing pressure can lead to changes in the biological characteristics of fish stocks, such as maturation, and thus these biological characteristics should be considered as variables rather than constants, as has often been assumed to be the case by managers.

It is therefore important that, when such data are not already available, managers should initiate sampling regimes and analyses aimed at determining whether the biological variables for a stock are changing and, if so, take the changes into account to ensure that stock assessments and management strategies for the future are robust.

Acknowledgments

Our gratitude is expressed to commercial fishermen O. McIntosh and W. Miller for sharing with us their knowledge of *Cnidoglanis macrocephalus*, based on many years of fishing for that species in Wilson Inlet, to K. Smith (Department of Fisheries, Western Australia), and to three anonymous reviewers, who provided constructive comments on our original submission. Funding was provided by the Fisheries Research and Development Corporation and South Coast Natural Resource Management, Inc. This project was approved by the Murdoch University Animal Ethics Committee (project numbers W1145-05 and W2183-08).

Literature cited

- Ayvazian, S. G., M. S. Johnson, and D. J. McGlashan. 1994. High levels of genetic subdivision of marine and estuarine populations of the estuarine catfish *Cnidoglanis macrocephalus* (Plotosidae) in southwestern Australia. *Mar. Biol. (Heidelberg, Ger.)* 118:25–31.
- Barot, S., M. Heino, L. O'Brien, and U. Dieckmann. 2004. Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. *Evol. Ecol. Res.* 6:659–678.
- Brander, K. M. 2007. The role of growth changes in the decline and recovery of North Atlantic cod stocks since 1970. *ICES J. Mar. Sci.* 64:211–217.
- Brown, C. J., A. J. Hobday, P. E. Ziegler, and D. C. Welsford. 2008. Darwinian fisheries science needs to consider realistic fishing pressures over evolutionary time scales. *Mar. Ecol. Prog. Ser.* 369:257–266.
- Cassoff, R. M., S. E. Campana, and S. Myklevoll. 2007. Changes in baseline growth and maturation parameters of Northwest Atlantic porbeagle, *Lamna nasus*, following heavy exploitation. *Can. J. Fish. Aquat. Sci.* 64:19–29.
- Cerrato, R. M. 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Can. J. Fish. Aquat. Sci.* 47:1416–1426.
- Chuwen, B. M., S. D. Hoeksema, and I. C. Potter. 2009a. Factors influencing the characteristics of the fish faunas in offshore, deeper waters of permanently-open, seasonally-open and normally-closed estuaries. *Estuar. Coast. Shelf Sci.* 81:279–295.
- 2009b. The divergent environmental characteristics of permanently-open, seasonally-open and normally-closed estuaries of south-western Australia. *Estuar. Coast. Shelf Sci.* 85:12–21.
- Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries over evolutionary time scales. *Science* 297:94–96.
- Conover, D. O., S. B. Munch, and S. A. Arnott. 2009. Reversal of evolutionary downsizing caused by selective harvest of fish. *Proc. R. Soc. Lond. B. Biol. Sci.* 276:2015–2020.
- Deriso, R. B., T. J. Quinn II, and P. R. Neal. 1985. Catch-age analysis with auxiliary information. *Can. J. Fish. Aquat. Sci.* 42:815–824.
- Dieckmann, U., and M. Heino. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. *Mar. Ecol. Prog. Ser.* 335:253–269.
- Ernande, B., U. Dieckmann, and M. Heino. 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. *Proc. R. Soc. Lond. B. Biol. Sci.* 271:415–423.
- Gabriel, W. L., and P. M. Mace. 1999. A review of biological reference points in the context of the precautionary approach. *In Proceedings of the fifth national NMFS stock assessment workshop* (V. R. Restrepo, ed.), p. 34–45. NOAA Tech. Memo. NMFS-F/SPO-40.
- Grift, R., A. Rijnsdorp, S. Barot, M. Heino, and U. Dieckmann. 2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Mar. Ecol. Prog. Ser.* 257:247–257.
- Heino, M. 1998. Management of evolving fish stocks. *Can. J. Fish. Aquat. Sci.* 55:1971–1982.
- Heino, M., U. Dieckmann, and O. R. Godø. 2002a. Measuring probabilistic reaction norms for age and size at maturation. *Evolution* 56:669–678.
- 2002b. Estimation of reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. *ICES J. Mar. Sci.* 59:562–575.
- Hilborn, R., and C. V. Minte-Vera. 2008. Fisheries-induced changes in growth rates in marine fisheries: are they significant? *Bull. Mar. Sci.* 83:95–105.
- Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull.* 82:898–903.
- Jørgensen, C., K. Enberg, E. S. Dunlop, R. Arlinghaus, D. S. Boukal, K. Brander, B. Ernande, A. Gårdmark, F. Johnston, S. Matsumura, H. Pardoe, K. Raab, A. Silva, A. Vainikka, U. Dieckmann, M. Heino, and A. D. Rijnsdorp. 2007. Managing evolving stocks. *Science* 318:1247–1248.
- Kirkwood, G. P., and T. I. Walker. 1986. Gill net mesh selectivities for gummy shark, *Mustelus antarcticus* Günther, taken in south-eastern Australian waters. *Aust. J. Mar. Freshw. Res.* 37:689–697.
- Laevastu, T. 1965. Manual of methods in fisheries biology, 50 p. FAO, Rome.
- Laurenson, L. J. B., F. J. Neira, and I. C. Potter. 1993a. Reproductive biology and larval morphology of the marine plotosid *Cnidoglanis macrocephalus* (Teleostei) in a seasonally closed Australian estuary. *Hydrobiologia* 268:179–192.
- Laurenson, L., I. Potter, R. Lenanton, and N. Hall. 1993b. The significance of length at sexual maturity, mesh size and closed fishing waters to the commercial fishery for the catfish *Cnidoglanis macro-*

- cephalus* in Australian estuaries. *J. Appl. Ichthyol.* 9:210–221.
- Laurenson, L. J. B., I. C. Potter, and N. G. Hall. 1994. Comparisons between generalized growth curves for two estuarine populations of the eel tailed catfish *Cnidoglanis macrocephalus*. *Fish. Bull.* 92:880–889.
- Law, R., and D. R. Grey. 1989. Evolution of yields from populations with age-specific cropping. *Evol. Ecol.* 3:343–359.
- Marshall, C. T., and H. I. Brownman. 2007. Introduction: Disentangling the causes of maturation trends in exploited fish populations. *Mar. Ecol. Prog. Ser.* 335:249–251.
- Melvin, G. D., and R. L. Stephenson. 2007. The dynamics of a recovering fish stock: Georges Bank herring. *ICES J. Mar. Sci.* 64:69–82.
- Morita, K., and M. Fukuwaka. 2007. Why age and size at maturity have changed in Pacific salmon. *Mar. Ecol. Prog. Ser.* 335:289–294.
- Neuheimer, A. B., and C. T. Taggart. 2007. The growing degree-day and fish size-at-age: the overlooked metric. *Can. J. Fish. Aquat. Sci.* 64:375–385.
2010. Can changes in length-at-age and maturation timing in Scotian Shelf haddock (*Melanogrammus aeglefinus*) be explained by fishing? *Can. J. Fish. Aquat. Sci.* 67:854–865.
- Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Brattey, B. Ernande, and U. Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428:932–935.
- Olsen, E. M., G. R. Lilly, M. Heino, M. J. Morgan, J. Brattey, and U. Dieckmann. 2005. Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 62:811–823.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Reznick, D. N., and C. K. Ghalambor. 2005. Can commercial fishing cause evolution? Answers from guppies (*Poecilia reticulata*). *Can. J. Fish. Aquat. Sci.* 62:791–801.
- Stearns, S. C., and J. C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* 40:893–913.
- Swain, D. P., A. F. Sinclair, and J. M. Hanson. 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proc. R. Soc. Lond. B. Biol. Sci.* 274:1015–1022.
- Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. *BioScience* 45:759–771.
- Venturelli, P. A., N. P. Lester, T. R. Marshall, and B. J. Shuter. 2010. Consistent patterns of maturity and density-dependent growth among populations of walleye (*Sander vitreus*): application of the growing degree-day metric. *Can. J. Fish. Aquat. Sci.* 67:1057–1067.