Rapid changes in life-history characteristics of a long-lived temperate reef fish

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Abstract. Banded morwong, Cheilodactylus spectabilis, a long-lived sedentary temperate reef fish, has undergone rapid changes in its growth and maturity characteristics along the east coast of Tasmania, Australia. Over a period of 10 years, growth of young males and females has consistently accelerated, such that in 2005, 3-year-old fish were up to 40 mm or 13\% longer compared with 1996, and age at 50\% maturity for females had declined from 4 to 3 years. The magnitude and speed of the observed changes were unexpected given the species’ longevity (maximum age of over 95 years). The underlying mechanisms for the changes remain unclear but density-dependent responses to changes in population size and age composition, possibly mediated through reduced competition for shelter and intra-specific interactions, may have been contributing factors. Increasing sea surface temperatures over part of the period of change does not appear to have been a major driver and a genetic response to fishing seems unlikely. Notwithstanding any uncertainty, C. spectabilis populations have become more productive in recent years, challenging the general approach towards stock assessment where life-history characteristics are assumed to remain stable across contrasting levels of stock abundance and environmental conditions.

Additional keywords: age structure, Cheilodactyliidae, density-dependence, growth, maturity, water temperature.

Introduction

Life-history characteristics, such as life-span, growth rates, natural mortality and age at maturity are related to each other and thought to be plastic and adaptable (Stearns and Crandall 1984; Wootton 1990). In fish populations, a range of factors have been found to influence these characteristics. Changes in the environment, particularly water temperature (Brett 1979; Brander 1995), or changes in population density (Helser and Almeida 1997; Godø and Haug 1999; Sánchez Lizaso et al. 2000; Lorenzen and Enberg 2002) can result in a phenotypic response, whereas fishing can act as an evolutionary force and cause genetic changes in growth and maturity (Grift et al. 2003; Olsen et al. 2005). Distinguishing phenotypic and genotypic effects is often difficult because their drivers apply at the same time and result in the same type of changes. However, it is important to separate and understand the underlying factors and their potential contribution to changes in life-history characteristics because growth and maturity, and hence the productivity of stocks experiencing exploitation, directly influence estimates of biomass in stock assessments. Whether changes are the result of phenotypic or genotypic effects could lead to different assumptions for future biomass projections and the potential development of the fishery.

Banded morwong, Cheilodactylus spectabilis (Hutton, 1872), are large, sedentary temperate reef fish that occur around southeastern Australia and New Zealand in shallow waters to at least 50 m depth (Gomon et al. 1994) and can reach ages of over 95 years (Ewing et al. 2007). With strong sexual dimorphism in growth, males grow substantially faster and to larger maximum sizes than females, although longevity is similar between the sexes. There is no information on the stock structure, but a long pelagic larval stage of around 6 months (Wolf 1998) suggests that single genetic stocks can occur over large areas. After settlement, populations are thought to mix little between reefs (Haddon et al. 2005) as a result of limited movement of adult fish (Murphy and Lyle 1999).

The species is commercially harvested in Tasmania and Victoria (Australia) by a small-scale coastal gill-net fishery. In Tasmania, the fishery is managed by a range of input controls, including limited entry, gear restrictions, keyhole size limits (360–460 mm fork length) and a seasonal spawning closure (Ziegler et al. 2005). The combination of growth rate differences between the sexes and the keyhole size limit has meant that fishing pressure is selectively greater for females, with few females ever exceeding the upper size limit. Fishers generally operate out of dinghies or small vessels and target C. spectabilis using large mesh gill-nets (130–140 mm mesh size) over shallow rocky reefs. Before 1990, the species had little commercial value apart from use as bait by rock lobster fishers. A targeted fishery started with the development of live fish markets in Australia in the early 1990s. Catches in Tasmania rose from less than 10 tonnes per annum before 1993 to a reported peak of 113 tonnes in 1994, although catches were probably overstated (Ziegler et al. 2005, Fig. 1). Reported catches then declined steadily to below 40 tonnes by 1999 and have since stabilised at around 40–50 tonnes per annum.
In the present study, we describe rapid changes in growth and maturity of *C. spectabilis* that have increased stock productivity and attempt to identify factors, particularly changes in water temperature and population density, which could have contributed to these observed changes.

**Materials and methods**

**Sampling**

Biological monitoring of *Cheilodactylus spectabilis* stocks was undertaken during the spawning season closure (March–April) in 1996 and 1997 and then annually between 2001 and 2005 inclusive. Two areas off the east coast of Tasmania, Tasman in the south-east and Bicheno in the central east (Fig. 2), were
The standard von Bertalanffy (VB) growth function described data according to the equation:
\[ L_t = L_\infty \left(1 + e^{-\alpha t}\right)^{-\frac{1}{c}} + \varepsilon \] (1)
where \( L_t \) is the length at age \( t \), \( L_\infty \) is the asymptotic length, \( \alpha \), \( b \), \( c \) and \( \varepsilon \) are parameters of the growth function, with \( b \) and \( c \) defining the shape of the function, and \( \varepsilon \) is a normal random residual error term with mean zero and standard deviation \( \sigma \). A sample of 10 recently settled juveniles, which had been collected from Bicheno in November 1996 and estimated to be around 6 months old, was added to the age samples of all years to anchor the growth functions at the youngest ages and sizes.

Regional growth patterns were compared using a likelihood ratio test for the growth function (Kimura 1980; Haddon 2001) in order to test the hypothesis that growth was similar between regions (Table 1). As a result of low and unequal numbers of fish older than 20 years between samples, these growth comparisons were restricted to fish up to 20 years of age.

Linear regression analysis of length at a given age class for different years was used to test for trends in size at age, with the focus on fish up to 10 years of age. Growth trajectories for individual cohorts were also examined using mean length at age from raw data.

### Growth comparisons

The standard von Bertalanffy (VB) growth function described the fast initial and subsequent slower growth phases for *C. spectabilis* poorly, resulting in highly skewed residuals (Ewing et al. 2007). Both a two-phase VB growth function, following a different function in each phase with a discontinuity at a transition age between the two phases (Soriano et al. 1992) and the generalised growth model of Schnute and Richards (1990) provided evenly distributed residuals in all samples. The latter model was used here because it was more robust and simplified the process of comparing between age samples. By minimising the negative log-likelihood, the model was fitted to length at age data according to the equation:

\[ L_t = L_\infty \left(1 + a e^{-\alpha t}\right)^{-\frac{1}{b}} + \varepsilon \] (1)

where \( L_t \) is the length at age \( t \), \( L_\infty \) is the asymptotic length, \( a \), \( b \), \( c \) and \( \varepsilon \) are parameters of the growth function, with \( b \) and \( c \) defining the shape of the function, and \( \varepsilon \) is a normal random residual error term with mean zero and standard deviation \( \sigma \). A sample of 10 recently settled juveniles, which had been collected from Bicheno in November 1996 and estimated to be around 6 months old, was added to the age samples of all years to anchor the growth functions at the youngest ages and sizes.

### Size and age at onset of maturity

In Tasmanian waters, *C. spectabilis* are in spawning condition between mid February and early May, with oocyte size distribution indicating that females are serial spawners (Murphy and Lyle 1999). A logistic function was fitted to the size at maturity or age at maturity of females using binomial residual errors:

\[ \mu_{l,y} = \frac{1}{1 + e^{-(a_l + b_y)}} \] (2)

where \( \mu_{l,y} \) is the predicted proportion at size or age class \( l \) in year \( y \) that is sexually mature, \( l \) is the length or age class, and \( a_l \) and \( b_y \) are the maturity parameters for each year \( y \). As sampling was conducted during the spawning season, immature and

<table>
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<th>Coincident (d.f. = 5)</th>
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Changes in life-history characteristics of *Cheilodactylus spectabilis*  

**Population size and age structure**

In the absence of reliable estimates of population size, standardized catch rates (*Ziegler et al. 2006*) were examined as a proxy for population biomass and used in conjunction with changes in population age composition to identify the potential for a density-dependent response of growth and maturity between 1996 and 2005. To assess relative changes in population age structure, age compositions based on the biological monitoring samples were adjusted for mesh selectivity. Mesh selectivity was estimated using the SELECT method (*Millar and Holst 1997*) from fishing trials involving five different mesh sizes. The gamma selection curve provided the best fit, presumably because many large fish were retained in the net mainly by wedging and tangling rather than gilling (*Ziegler et al. 2006*). Relative gill-net selectivity peaked around 395 mm and exceeded 50% for fish between 280 and 510 mm, indicating that selectivity was relatively high for fish older than 3 years of age (refer to Results).

**Results**

**Growth comparisons**

By sex, functions describing the first 20 years of growth did not differ significantly between sampling regions in four out of the 6 years investigated (Table 1). For males, the parameter $a$ differed between the regional samples in 1997, whereas for females $L_\infty$ differed between regions in 1997 and 2005. Relatively small sample sizes and uneven spread of ages appear to have contributed to the apparently anomalous findings in 1997 and 2005. Since growth did not differ between regions within most years, pooling of regional samples appeared justified.

Length at age was generally comparable between the sexes up to ~5 years of age after which males tended to be larger at age than females (Fig. 3). A general acceleration of growth in the younger age classes was evident over the sampling period. This acceleration was most pronounced for 3 year olds, which increased in mean length at a rate of almost 5 mm per year over the sampling period for both sexes. The rate of increase declined gradually for older age classes, although mean size estimates became noisier as a result of smaller sample sizes among the older age groups. Between 4 and 7 years the rate of increase was generally higher for males, at almost 4 mm per year compared with around 3 mm per year for females. There was no significant growth increase evident in fish 10 years of age or older.

The observed changes in growth were consistent over time and apparent in all cohorts recruiting to the fishery in recent years (Fig. 4). Individuals from cohorts born before 1994 and available to the fishing gear by 1997 (i.e. ≥3 year olds), remained smaller on average than those recruiting to the fishery in subsequent years. Similarly, cohorts born after 1999 and recruiting to the fishery in the early 2000s tended to be slightly larger, on average, than cohorts born between 1997 and 1999.

Growth functions fitted to the length at age data also reflected these changes in growth (Fig. 5), with significant differences of growth e.g. between 1996 and 2001 (likelihood-ratio test: males: all parameters $P < 0.001$; females: $L_\infty$ and $a$: $P < 0.05$) and between 2001 and 2005 (males: all parameters $P < 0.001$; females: $L_\infty$: $P < 0.001$; $b$, $c$ and $a$: $P < 0.05$).

**Size and age at onset of maturity**

Age at 50% maturity in females fell from around 4 years in 1996–1997 to below 3 years by the early 2000s (Fig. 6; Table 2). The logistic function also became increasingly steeper indicating that maturation occurred more rapidly across the population in recent years. In the combined 1996–1997 sample, age at first maturity was 4 years with most females mature by 8 years of age. By contrast, since 2001 the age at first maturity had fallen to just 2 years, with most females mature by 4 years. Size at maturity also varied through time, with size at 50% maturity declining from around 325 mm in 1996–1997 to below 320 mm in 2001 and then to 305 mm in 2002–2003. However, in 2004–2005 the size at maturity had returned to a level similar to that observed in 2001; this increase appears to be a result of the increased size at age by 2004–2005.
Growth correlations with water temperature

Daily sea surface temperatures near both sampling regions generally increased during the latter half of the 1990s and peaked in 2000–2001 (Fig. 7a). Between September 1995 and February 2001, spring SSTs increased by an average 0.34°C per year in the Tasman (regression analysis: \( n = 546, t = 17.0, P < 0.0001 \)) and 0.29°C in Bicheno (\( n = 546, t = 12.7, P < 0.0001 \)). Summer temperature increases were greater, at 0.54°C per year in Tasman (\( n = 542, t = 16.6, P < 0.0001 \)) and 0.50°C in Bicheno (\( n = 542, t = 16.5, P < 0.0001 \)). Since 2001 seasonal SSTs have fluctuated without obvious trend.

Standardised annual growth increments for males and females were not significantly correlated with local mean spring or summer sea surface temperatures, with the exception of a weak positive correlation between growth for males and spring temperatures (Fig. 7b; regression analysis, \( n = 31, F = 5.0, P = 0.03; P > 0.05 \) for all other regression analyses).

Population size and age structure

Commercial catches and standardised catch rates declined sharply from the mid-1990s to 2000, implying a strong fishery impact on Cheilodactylus spectabilis stocks. Since 2001,
Changes in life-history characteristics of *Cheilodactylus spectabilis*

**Fig. 4.** Mean length at age for *Cheilodactylus spectabilis* cohorts born between 1992 and 2002 (samples with at least four individuals at age are shown). For clarity, some cohorts have been omitted and different length scales are used for males and females. Birth years are indicated.

**Fig. 5.** Schnute and Richards (1990) growth functions for *Cheilodactylus spectabilis* fitted to the samples taken in 1996, 2001 and 2005. Growth functions for both sexes were significantly different between 1996 and 2001, and between 2001 and 2005 (likelihood ratio test, see text).

however, catches stabilised and catch rates recovered to slightly below initial concentrations (Fig. 1). Recent increases in catch rates suggest that the initial fishing down of the populations may have been compensated to some extent by recruitment in recent years. Changes in age composition corrected for mesh selectivity tend to support this observation, with the proportion of young fish increasing in the more recent samples (Fig. 8). The relative proportion of females older than 10 years by number was estimated to have declined from 66% in 1996 to just 35% by 2005. Median age also fell from 19 to 22 years in the mid-1990s to 6–7 years since the mid-2000s, with individuals 7 years of age and younger dominating the population in 2005. Changes in age structure for males were not as marked. The relative proportion of males older than 10 years declined from 48 to 35% between the mid-1990s and the mid-2000s, with median age falling from 7–8 to 5 years over the same period.

**Discussion**

The present study has demonstrated that *Cheilodactylus spectabilis* populations along the east coast of Tasmania have undergone a rapid change in their growth and maturity characteristics. Early growth of males and females had accelerated over a 10-year period such that 3-year-old fish were close to 40 mm, or 13%, larger in 2005 compared with 1996, and age at 50% maturity for females had fallen by over a year. The magnitude
and speed of the observed changes were unexpected and imply that the species is flexible in its life-history characteristics. This flexibility needs to be considered in the context of an extremely long-lived species with a maximum age of over 90 years, which clearly exhibits characteristics of a short-lived species with rapid early growth and early age at maturity.

The growth acceleration was reflected in age classes up to at least 7 years of age and could be tracked over time for the cohorts born since 1990. By 10 years of age, differences were not significant, which is consistent with the general slowing of growth towards an asymptote. However, if these growth changes are only a recent phenomenon, the impact of faster growth rates on the older age classes may yet be observed in the population. Coincident with increased growth, the location and shape of the age at maturity function shifted to younger ages and increased in steepness. Most females were fully mature at 4 years of age by the mid-2000s, compared with around 8 years during the mid-1990s. The age at 50% maturity fell from 4 to 3 years over this period, with some individuals mature at just 2 years of age in the most recent samples. The main shift in age at maturity occurred...
Changes in life-history characteristics of *Cheilodactylus spectabilis*  

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between 1996–1997 and 2001, the years following the largest reported commercial catches and a sharp decline in catch rates. Since 2001, age at maturity has changed little, suggesting that it may have reached a lower limit of possible change. Size at maturity showed a similar initial decrease, but increased slightly in the most recent years sampled, a consequence of the continued increase in growth rates of the younger age classes. Such co-occurring changes in growth and size and age at maturity, as observed here for *C. spectabilis*, are common among a range of fish species (Trippel 1995; Rochet 1998; Sánchez Lizaso et al. 2000), since many life-history characteristics are related to body size. As a result, maturation does not necessarily occur at a fixed size or age for many species.

Environmental factors such as water temperature can influence growth in a population (e.g. Brander 1995; Pörtner et al. 2001). Using otolith structure, Thresher et al. (2007) inferred that growth of *C. spectabilis* had generally increased in response to rising water temperatures over a period of 80 years (up to the early 1990s). For the first half of the decade covered by the present study, spring and summer water temperatures on the east coast of Tasmania increased and then fluctuated without obvious trend for the second half. Although a weak correlation between growth increments and mean spring sea surface temperatures was evident for males up to 6 years of age, there was no such correlation for summer temperatures. Variability in female growth increments was not correlated with either spring or summer water temperatures. Furthermore, the observation that overall growth patterns were similar between the two sampling regions, even though sea surface temperatures varied by $\sim 0.5–1.0^\circ C$, suggests that water temperature changes were unlikely to have been the major driver for the observed growth acceleration.

Changes in population density, particularly a fishery-induced reduction in stock biomass, can lead to a density-dependent response, with faster growth of individuals at smaller stock sizes (Helser and Almeida 1997; Gode and Haug 1999; Sánchez Lizaso et al. 2000; Rose et al. 2001; Lorenzen and Enberg 2002). Catch rates for *C. spectabilis* provided no clear indication that overall stock biomass had undergone a substantial decline. Although catch rates declined initially, they have increased since the early 2000s as catches stabilised at relatively low concentrations. However, catch rates can be a poor predictor of stock abundance for sedentary species such as *C. spectabilis* since serial depletion can mask depletion effects leading to overestimates of biomass (Ziegler et al. 2005).

Despite uncertainty about biomass, population age structure has undergone some major changes, with younger age classes becoming increasingly dominant in the population. These changes were more conspicuous for females, a consequence of greater susceptibility to the fishery arising from slower growth rates and an upper size limit that few females actually attain (Ziegler et al. 2005). By contrast, faster growth rates and larger sizes for males mean that most individuals are vulnerable to the fishery for less than 10 years. Age structure changes imply that the fish-down of accumulated biomass in older age classes has been compensated to some extent by recruitment. Unfortunately, in the absence of a reliable index of abundance, it is not possible to quantify the magnitude of recent recruitment events based on age structure information alone. However, unusually strong recruitment events appear unlikely in the context of the observed ongoing increases in growth rates. Rather, life time growth of particularly strong cohorts is typically slower in fishes, presumably the result of increased competition for resources (Punt and Smith 2001; Punt et al. 2001).

Changes in the population structure could provide an explanation for the observed changes in growth and maturity, based on reduced competition particularly for shelter space. *Cheilodactylus spectabilis* populations are structured by sex, size and depth, with individuals settling into the shallow parts of a reef

### Table 2. Sample sizes for the proportion of mature female *Cheilodactylus spectabilis* by age (years) and size (pooled into 10 mm classes)

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and gradually moving into deeper water thereafter (McCormick 1989a). This trend is more accentuated for males, resulting in a dominance of large males in deeper areas, whereas females are more common at mid-depths. Only adult males exhibit defensive territorial behaviour towards conspecifics of similar size, defending shelter and patches of reef at least during the spawning season when females move to caves occupied by males for spawning (McCormick 1989b). The importance of shelter was highlighted for the closely-related red morwong *Cheilodactylus fuscus*, where removal of large individuals by spear fishing led to the quick occupation of freed-up shelters by the remaining fish or fish that had newly moved into the area (Lowry and Suthers 2004). This implies an obstruction exhibited by the established population towards emerging fish, despite the lack of aggression or territoriality observed between conspecifics. Both young males and females could profit from decreased intraspecific competition at lower stock concentrations by increasing growth and survival success. In addition, intense pairwise mating interactions between females and large males (McCormick 1989b), as well as reduced suppression of onset at maturity for small females by the presence of larger females may play a role in the earlier onset of maturity.

Major competitive pressure for food appears less likely, given that *C. spectabilis* are micro-carnivores and feed, with some...
degree of prey selectivity, mainly on highly abundant gammarid amphipods, ophiuroids and polychaetes (McCormick 1998). In addition, intra-specific competition for food between small and large fish is reduced, because prey size is linked to fish size even though juveniles and adult fish target similar prey species. Fish larger than 200 mm, including ages of 2 years and greater, cover foraging areas, which tend to overlap between individuals, reflecting a low degree of exclusive feeding areas and site-associated aggressive behaviour (Leum and Choat 1980).

A genotypic change of a life-history characteristic occurs when non-random fishing mortality applies to the fish population, typically by selection of a particular size range (Grift et al. 2003; Engelhard and Heino 2004; Olsen et al. 2005). For example, high fishing mortality of larger fish in a population can select for fish that mature at a younger age and smaller size, because bringing maturation forward increases the probability of successful reproduction. Such a genetic change as a result of fishing pressure has been suggested for the red porgy (Pogrus pagrus; Harris and McGovern 1997), North Sea plaice (Pleuronectes platessa; Grift et al. 2003), American plaice (Hippoglossoides platessoides; Barot et al. 2005) and several North Atlantic and North-east Arctic cod stocks (Gadus morhua; Heino et al. 2002; Olsen et al. 2005). There are several reasons indicating that a genotypic change in growth and maturity is less likely for C. spectabilis. First, the time span of just 5–10 years over which the changes occurred appears extremely short for a genotypic change. This is equivalent to less than two generations and much less than generally advocated as being a minimum period required for evolutionary changes. Changes in growth have been observed within as few as three to four generations in the laboratory (Conover and Munch 2002), but it remains to be proven whether such a process would operate similarly in real fisheries. Second, whereas fast-growing males are less susceptible to fishing and less likely to be removed because they pass through the size limit range of 360–460 mm more quickly than slower growing individuals, females remain effectively vulnerable for the rest of their lives once they have recruited to the fishery. Size-selection would therefore be expected to favour slow-growing females, which do not reach the minimum size limit as quickly as fast-growing individuals.

Discriminating between phenotypic and genotypic trends is important, because growth and maturity are major factors that determine the productivity of fish stocks. Although long recovery times are expected once genotypic changes occur (Law 2000), phenotypic trends tend to be reversible when conditions change again. Few studies have explicitly incorporated density-dependent mechanisms into stock assessments when projecting future biomass and harvest strategies (Helser and Brodziak 1998). Although trends in growth and maturity, by way of growth and logistic maturity functions, can be incorporated into a historical assessment of the C. spectabilis fishery, projections for the future development of the biomass without the knowledge...
of the potential density-dependent mechanisms would result in increased uncertainty. Should only the most recent patterns of growth and maturity be used, then such stock projections are likely to be overly-optimistic when stock biomass is expected to rise again.

Changes in growth and maturity as found for *C. spectabilis* have several important consequences for fisheries monitoring and assessment. First, there is a need to anticipate that even long-lived species can be flexible in their life-history characteristics and that significant changes can occur over relatively short periods. Second, it is important to track growth and maturity repeatedly through the course of a fishery because of the potential effects on population productivity and implications for stock assessments. However, the provision of on-going research funding for small-scale fisheries such as that for *C. spectabilis* will often be difficult to justify based on fishery value. Finally, our findings also challenge the general approach towards stock funding for small-scale fisheries such as that for *Pagrus pagrus*, from the southeastern United States, 1972–1994. *Fishery Bulletin* 95, 732–747.


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