

**Fig. 6.** Proportion of mature female *Cheilodactylus spectabilis* by age (left) and size (right). Fitted logistic function (solid line) to data (filled circles; size data presented in 10 mm size classes) combined from both regions and pooled into the periods 1996–1997, 2001, 2002–2003 and 2004–2005. As a reference, the function fitted to the data from 1996–1997 is shown as dotted line. The vertical line represents the age or size at 50% maturity.

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

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

Overall sample sizes were higher for size at maturity because sizes up to 400 mm represented also ages well over 15 years

Age (years)	1996–1997	2001	2002–2003	2004–2005	Size (mm)	1996–1997	2001	2002–2003	2004–2005
1	0	0	1	0	250	1	1	3	0
2	2	13	13	5	260	3	0	1	0
3	5	21	22	6	270	1	3	0	0
4	16	2	35	26	280	2	1	3	2
5	44	2	26	10	290	3	5	7	0
6	12	6	3	6	300	2	8	9	2
7	5	10	6	10	310	5	5	8	3
8	5	2	7	2	320	9	6	10	0
9	12	2	2	0	330	17	11	25	2
10	6	7	2	1	340	24	16	31	24
11	2	4	10	1	350	24	11	44	19
12	4	2	4	1	360	30	22	39	31
13	2	4	2	2	370	21	27	21	34
14	4	0	0	1	380	39	24	36	36
15	1	1	2	1	390	53	23	29	45
					400	48	24	22	34
Total	120	76	135	72	Total	282	187	288	232

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 were 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 ~0.5–1.0°C, suggests that water temperature changes were unlikely to have been the major driver for the observed growth acceleration.

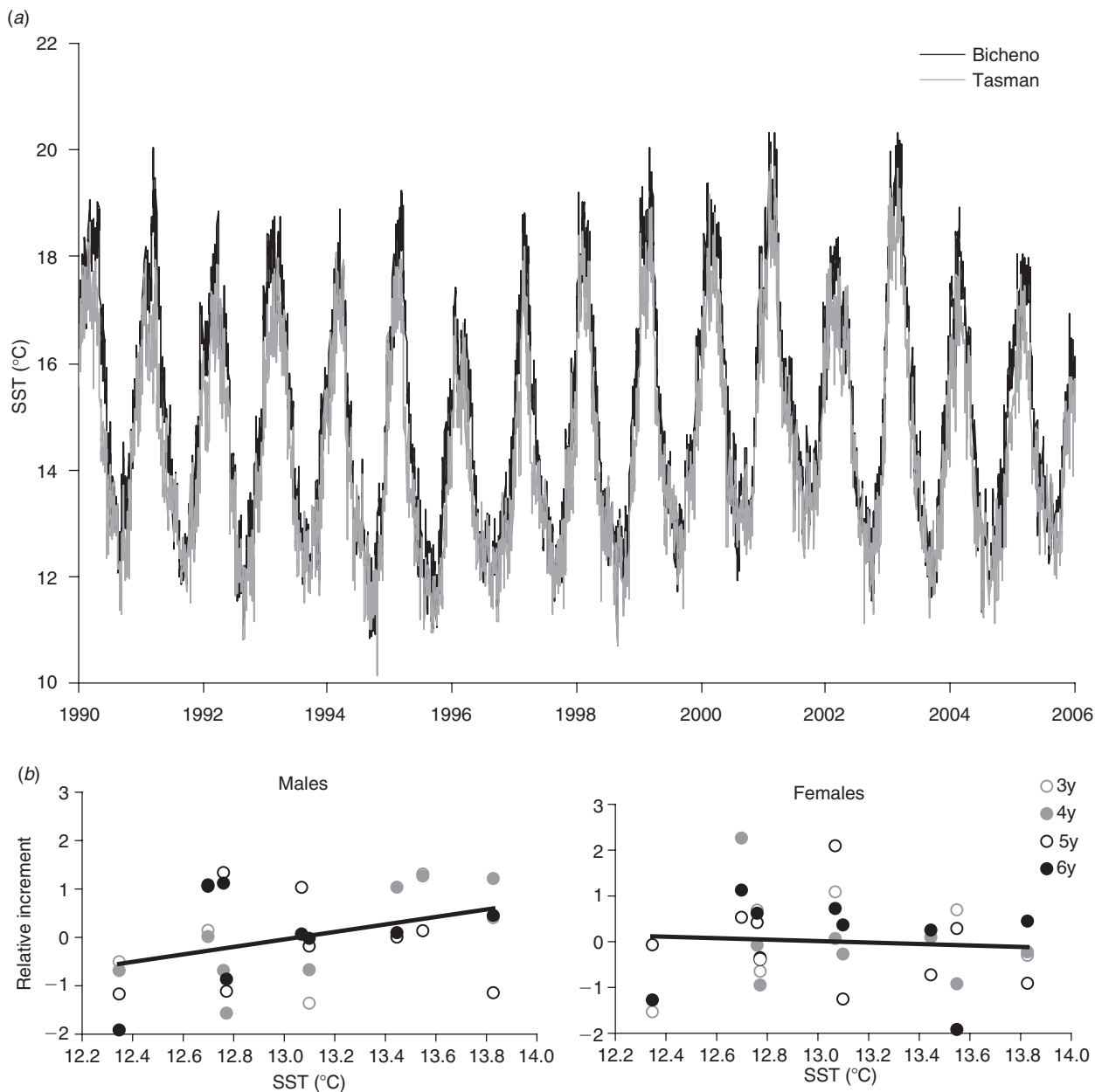
Changes in population density, particularly a fishery-induced reduction in stock biomass, can lead to a density-dependent response, with faster growth of individuals at smaller stock

sizes (Helsler and Almeida 1997; Godø 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



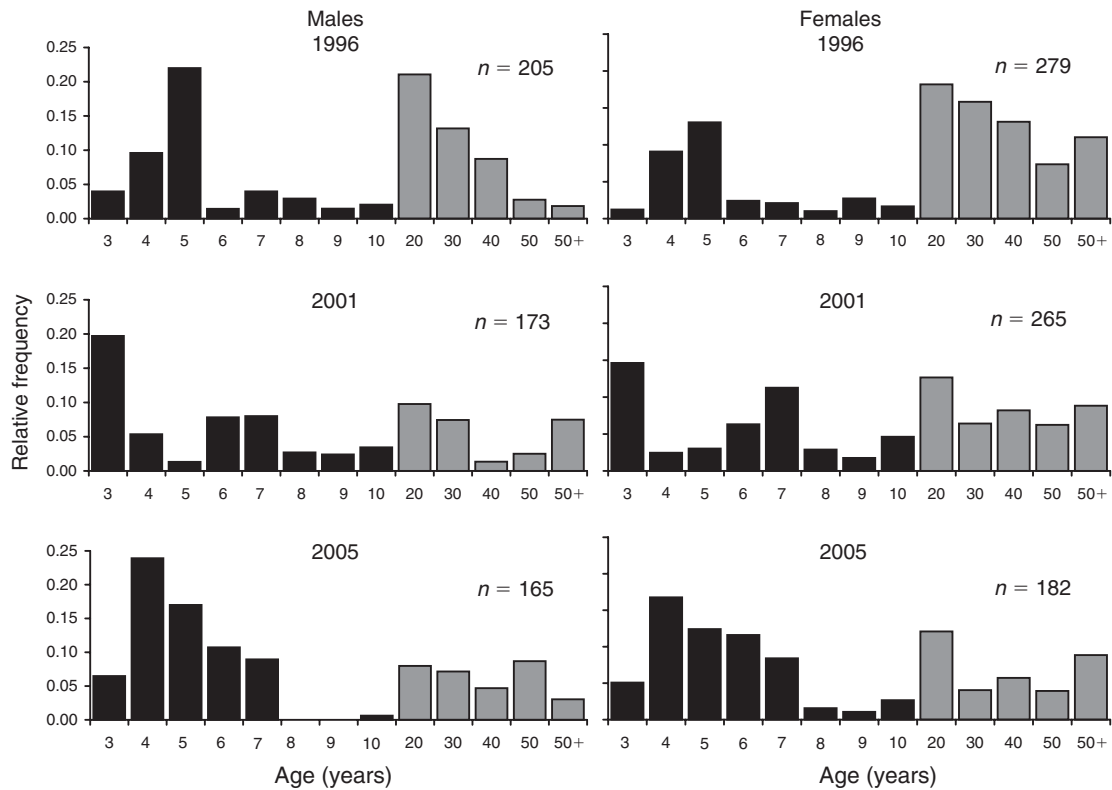


**Fig. 7.** (a) Daily sea surface temperatures (SST) near the Bicheno (black) and Tasman sampling regions (grey) from 1990 to 2005; and (b) regression plots of standardised annual growth increments for 3–6 year olds versus SST in spring for male and female *Cheilodactylus spectabilis*.

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



**Fig. 8.** Estimated age composition of the male and female *Cheilodactylus spectabilis* populations in 1996, 2001 and 2005, based on the pooled age composition from the biological monitoring in the Tasman and Bicheno regions and adjusted for mesh selectivity. Relative frequencies of 1-year classes (black bars, ages 2–10 years), 10-year classes (grey bars, ages 11–50 years, values given denote upper limit) and a plus group for fish older than 50 years (grey bar, denoted as 50+).  $n$  is sample size.

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 (*Pagrus 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 assessment where life-history characteristics are assumed to remain stable across contrasting levels of stock abundance and environmental conditions.

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