Social Inhibition of Maturation in Females of the Temperate Wrasse

*Pseudolabrus celidotus* and a Comparison with the Blennioid *Tripterygion varium*

G. P. Jones and S. M. Thompson

University of Auckland, Marine Research Laboratory; R.D., Leigh, Auckland, New Zealand

Abstract

In two temperate reef fish, *Pseudolabrus celidotus* (Bloch and Schneider) and *Tripterygion varium* (Bloch and Schneider) studied near Leigh, New Zealand, most spawning activity was concentrated during the first 2 months of spawning seasons which lasted about 5 months. In *P. celidotus*, maturation and spawning of first-year females (0+) was delayed with respect to older (>1+ yr) females. Within the 0+ age class, the minimum size of maturation declined as the spawning season proceeded. However, in all females of *T. varium*, ripening and spawning took place over the same time ranges. Observations on the seasonal patterns of female aggression suggested that larger female *P. celidotus* were socially inhibiting the maturation of small females. The level of interaction was high compared to that in *T. varium*, and reached a peak over the onset of the spawning season. This hypothesis was tested by the removal of larger (>1+ yr) female *P. celidotus* from a field population. The remaining 0+ females increased in ovary weight and matured earlier than those in an undisturbed area. We argue from this experiment that it is of advantage for *P. celidotus* females to spawn early in the season and of advantage to inhibit other females from doing so. Two possible reasons are suggested, the first applying to sex-changing species such as *P. celidotus*, the second to temperate-water fishes in general.

Introduction

Most studies on the spawning seasons of fishes have been limited only to a general description. The timing of spawning activity within the spawning season has received little attention. Nevertheless, it has been argued that for a female, fitness is extremely sensitive to the precise moment and circumstances for converting eggs to zygotes (Williams, 1975). The entire season may not be equally favourable for fertilization in terms of growth and survival of offspring (Perrins, 1970). Also, the fitness of a female may be affected by the timing of spawning relative to conspecifics, within the limits imposed by the environment.

In a number of fish species, larger females ripen and spawn before smaller ones (Healey, 1971; Staples, 1975; Merriner, 1976). This pattern is also common in birds (see references cited in Perrins, 1970). There are two hypotheses which could account for this pattern: (1) Maturity could be size-dependent and smaller females might not reach the critical size until later in the spawning season. (2) It could be of advantage to spawn before other females early in the season; larger females may socially inhibit the ripening of smaller females. In fishes, social inhibition of maturation has been demonstrated only in males of the freshwater genus *Xiphophorus* (Sohn, 1977; Borowsky, 1978) and hermaphrodites of the coral-reef anemonefish genus *Amphiprion* (Fricke and Fricke, 1977; Moyer and Nakazono, 1978). However, it has been shown that aggressive activity of adult females suppresses maturation of female offspring in family groups of the small mammal *Meriones unguiculatus* (Payman and Swanson, 1980).

The purpose of this paper is to assess the importance of aggressive interactions between females in affecting size-related onset of spawning in two temperate reef fishes with differing mating and social systems. Firstly, it was necessary to describe the seasonal patterns of spawning. For each species we asked, what was the length of the spawning season and, within these limits, when did most of the spawning activity occur? Secondly, do larger females ripen and/or spawn before smaller females? To establish whether social inhibition was implicated in size-specific maturation, we then looked at female spatial patterns and the seasonal levels of inter-female aggression. Where social inhibition was suggested, we examined the hypothesis by the experimental removal of mature females in a field population and compared the rate of maturation of first-year females with that in an undisturbed area.
The species chosen were the protogynous wrasse *Pseudolabrus celidotus* (Labridae) and the small blennioid fish *Tripterygion varium* (Tripterygiidae). In *P. celidotus* (Jones, 1980), females and territorial terminal-phase males pair-spawn, releasing their gametes 1 to 2 m above the substratum. The female or initial coloration is also distinguished by a number of small males. Females mature in their first (0+) year. By age 4+, most females have changed sex and colour, and males have been found as old as 8+ and as large as 230 mm (standard length). In *T. varium*, females lay eggs on bare rock surfaces in the territories of males (Thompson, 1979). Males guard the nests until the eggs hatch; they exhibit secondary sexual colours only during the spawning season. Both males and females mature in their first year and may reach 2+ yr old and a size of 100 mm. In *P. celidotus* and *T. varium*, females aged 0+ and ≥1+ yr are readily distinguished in the field.

Materials and Methods

**Sampling and Description of Oogenesis**

*Pseudolabrus celidotus* (Bloch and Schneider) were collected at approximately monthly intervals from January 1976 until September 1977 from shallow-reef areas near Goat Island, Leight (174°48'E; 36°17'S), 90 km north of Auckland, New Zealand. These samples have been the material of a general study on the growth and reproductive biology of this species, and Jones (1980) gives the general methods of fish collection, processing, age determination and gonad sectioning. *Tripterygion varium* (Bloch and Schneider) were collected from the same locality at monthly intervals from February 1977 until September 1978. These also have been used in a study of growth and reproduction (Thompson, 1979). The present paper makes use of the samples of females to describe oogenesis.

Oogenesis was divided into the following stages (see Moe, 1969 for histological descriptions):

**Stage 1.** Early oocytes. In *Pseudolabrus celidotus* these were 15 to 45 µm in diameter; in *Tripterygion varium* 25 to 50 µm d.

**Stage 2.** Resting, previtellogenic oocytes. In *Pseudolabrus celidotus* 45 to 70 µm d; in *Tripterygion varium* 50 to 150 µm d.

**Stage 3.** Early vitellogenic oocytes. In *Pseudolabrus celidotus* 70 to 150 µm d; in *Tripterygion varium* 150 to 250 µm d.

**Stage 4.** Vitellogenic oocytes. In *Pseudolabrus celidotus* 130 to 350 µm d; in *Tripterygion varium* 250 to 370 µm d.

**Stage 5.** Mature oocytes = eggs. In *Pseudolabrus celidotus* up to 800 µm d; in *Tripterygion varium* up to 1,300 µm d.

The state of development of each ovary was measured by an assigned developmental class based on the predominant stage of oogenesis. The classes adopted were derived from Moe (1969), with the following modifications: (1) Immature females could not always be distinguished from mature, unripe females because atretic bodies were only occasionally present in the latter; both were given the same classification. (2) A ripening phase was recognized. The classification was as follows:

- **Class 1.** Immature females and mature unripe females — Oocyte Stages 1 and 2 predominated (in terms of surface area of sections), with Stage 3 rare.
- **Class 2.** Ripening females — Oocyte Stage 3 Predominated, but all stages were usually present.
- **Class 3.** Mature, ripe females — Oocyte Stage 4 predominated, but all stages were usually present. Eggs predominated when females were ready to spawn, but this stage was apparently brief.
- **Class 4.** Postspawning females — the ovary was dispersed, with many empty follicles and degenerating Stage 3 and 4 oocytes. Stages 1 and 2 were proliferating.

**Behaviour**

Observations upon each species were divided into two categories: (1) Measurements of how the rate of spawning was distributed over the spawning season, and observations of the seasonal differences in the spawning of 0+ and ≥1 + yr females. For this purpose, attention was directed at males since spawning activity was confined to the territories of certain males in both species and females made temporary trips to these areas. (2) Observations on females to determine how much of their time budget was spent on aggressive interactions with other females and juveniles and to determine how females were spaced with respect to each other.

Behaviour was studied in a shallow-water area called Waterfall Reef, by Goat Island (Fig. 1, Site A). The habitat was characterized by urchin (*Evechinus chloroticus*)-grazed bare-rock flats and dissected rock areas (Ayling, in press). Boulders of various sizes (up to 5 m across) were scattered throughout the area, often covered with patches of the laminarian kelp *Ecklonia radiata* and a number of fucoid species, mainly *Carpophyllum angustifolium*. Towards shallower water, fucoids predominated, urchins were more patchy and rock flats were more often covered with a low turf of the crustose red alga *Corallina officinalis*. The study of *Pseudolabrus celidotus* behaviour was made within a 8,000 m² mapped area which ranged from 0 to 10 m in depth. *Tripterygion varium* observations were made in a small broken site within the above area. This 45 m² area was mapped in finer detail.

Both species were watched monthly while SCUBA-diving. *Pseudolabrus celidotus* were observed from October 1977 until September 1979 and *Tripterygion varium* from February 1978 until February 1979. Observations on equivalent months in successive years were pooled for all analyses. Individuals were identified on the basis of size estimates and variations in the lateral and frontal (between the eyes) coloration.