A FIELD STUDY OF
TERRITORIAL AND
REPRODUCTIVE BEHAVIOUR
OF THE CUNNER,
TAUTOGOLABRUS ADSPERSUS,
IN CONCEPTION BAY,
NEWFOUNDLAND

ROBERT ARTHUR POTTLE

National Library of Canada

Cataloguing Branch
Canadian Theses Division

Ottawa, Canada
K1A 0N4

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

Bibliothèque nationale du Canada

Direction du catalogage
Division des thèses canadiennes

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

NL-339 (3/77)

A FIELD STUDY OF TERRITORIAL AND REPRODUCTIVE BEHAVIOUR OF THE CUNNER, *Tautogolabrus adspersus*, IN CONCEPTION BAY, NEWFOUNDLAND

by

© Robert Arthur Pottle, B. Sc.

A Thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

Department of Biology
Memorial University of Newfoundland
November 1978

St. John's Newfoundland

ABSTRACT

Territorial and reproductive behaviour in the cunner, Tautogolabrus adspersus (Walbaum), were observed in Conception Bay, Newfoundland. Cunners are active from May until November and spend the winter months in a state of torpor in the substrate. Males more than 6 years old establish territories in early June. Territories are defended outside the mid-summer spawning season. Both territorial and nonterritorial males of >150 mm TL acquire nuptial colouration between emergence from overwintering torpor and the start of the spawning season. Nonterritorial males are vigorously excluded from territories by the resident males and appear to contribute little to the reproductive effort of the population. Territorial females are found in the peripheral areas of some males' territories and exhibit aggressive behaviour toward other females. Both territorial and nonterritorial females pair spawn with territorial males. Fish of both sexes are capable of multiple spawns. Group spawning by nonterritorial cunners was not observed. The function of territory defense in T. adspersus is discussed.

ACKNOWLEDGMENTS

The author wishes to thank Andrew Turner and David Martin for their patience and valuable assistance during field observations. John Barrie, Gregory Goff, and Michael McGurk assisted with other aspects of the field work. I am grateful to Drs. B. Kim and J. Rice for advice on statistical matters and to Roy Ficken for photographic work in the preparation of figures. Drs. J. Lien and J. Rice kindly reviewed the manuscript. Special thanks are due to Dr. John M. Green, my supervisor, for his sustained interest and support, and to Moya Walsh, who typed the manuscript. Financial support was provided by a fellowship from the Department of Graduate Studies and by an operating grant to Dr. J. M. Green from the National Research Council of Canada.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The cunner, Tautogolabrus adspersus (Walbaum) is the only member of the Labridae, an essentially tropical and warm temperate family, found in Newfoundland waters. The species ranges from the mouth of Chesapeake Bay to the Strait of Belle Isle and is common on shallow inshore reefs, shelterered rock substrates and wrecks, and near wharves. Such habitats provide both shelter for protection during nocturnal quiescence and overwintering torpor and a suitable substrate for the benthic organisms on which cunners feed.

Although abundant and easily accessible throughout its range, T. adspersus has been the subject of few behavioural or ecological studies, principally because the species lacks commercial importance. However, due to its year-round association with a relatively small home range (Green, 1975; Olla et al., 1975) the cunner has potential as an indicator of inshore environmental perturbations, as demonstrated by Payne (1976).

On the southeastern coast of Newfoundland cunners are active primarily from late May until early November, although a few fish may be seen a few weeks earlier or later. It was once thought that T. adspersus migrated to deeper, warmer water for the winter months (Ambrose, 1870; Bigelow and Schroeder, 1953). A physiological study by Haugaard and Irving (1943) indicated that cunners could not remain active at normal inshore winter temperatures and added credence to the theory. However, field observations have shown that cunners overwinter inshore in a state of torpor (Green and Farwell, 1971; Dew, 1976). When water temperature falls below 5 - 6°C, cunners cease feeding and seek shelter in narrow crevices in the substrate. T. adspersus can withstand prolonged exposure to water temperatures below 0°C, as attested by its year-round presence in inshore Newfoundland waters. The period of inactivity varies from 3 - 4 months off Connecticut (Dew, 1976) to 5 - 6 months off Newfoundland. Cunners emerge from their torpid state when water temperature again reaches 5 - 6°C.

T. adspersus feeds primarily upon molluscs and benthic crustaceans, including mussels, limpets, chitons, mysids and amphipods, although a variety of other invertebrates, both benthic and planktonic, are consumed (Olla et al., 1975; Shumway and Stickney, 1975; Dew, 1976). Essentially opportunistic feeders, cunners also consume carrion and fish offal.

Nocturnal quiescence is a general feature of labrid behaviour (Hobson, 1965, 1972; Reinboth, 1973; Roede, 1972). The cunner is active only during daylight hours and spends the night in shelter on the substrate. At night, cunners are in a quiescent state characterized by a marked reduction of responsiveness to external stimuli (Olla et al., 1975; Dew, 1976). During field studies by Olla et al. (1975) tagged fish became quiescent 5 - 55 min before the end of evening civil twilight and became active 16 - 41 min after the start of morning civil twilight.

On the basis of aquarium observations of a juvenile cunner, McErlean (1963) suggested that the species might be territorial. The first field observations of both territorial and reproductive behaviour were reported in a brief note by Wicklund (1970). Group spawns by aggregations of 3 - 15 cunners in the 75 - 125 mm TL ranges had been seen off New Jersey in June and July, 1963. Larger fish of 150 - 250 mm TL actively defended territories but did not participate in spawning activity. To date, no further descriptions of cunner territorial and reproductive behaviour have been published.

The presence of territorial cunners in Newfoundland waters was suspected following homing experiments conducted in 1973 – 1974, and confirmed during 1975 field studies (Green, unpublished data). In contrast to Wicklund's observations, pair spawning by territorial fish was the only form of reproductive behaviour observed.

The objectives of this study were to provide a detailed account of spawning and territory defense in T. adspersus and to determine the function of territorial behaviour in this species.

MATERIALS AND METHODS

Study site

All behavioural data were collected in situ at Broad Cove, Conception Bay, Newfoundland (Lat. 47°35' N, Long. 52°53' W). Although searches for tagged fish covered most of the cove to a depth of 10 m, primary data collection was confined to a 30 X 40 m area ranging in depth from 2.5 - 6.5 m (MLW) (Figure 1).

Bottom topography in the area was representative of the cove in general, consisting of bedrock outcrops interspersed with expanses of large and small boulders. The bottom sloped gradually seaward to the outer edge of the study site, a sharp drop from the 4 to the 6.5 m contour.

Depth was sufficient to prevent disturbance of fish by snorkelling observers, yet shallow enough to permit recognition of individual fish during daylight under all but extremely turbid conditions. Strong wave-associated bottom turbulence was rare, and occurred only when wave height was 1 m or greater.

More than 10 male T. adspersus defended territories within the area, and an overwintering site was situated 10 - 20 m seaward of its outer perimeter.

Data collection

Twenty-four preliminary SCUBA and snorkel dives were made between late April and early July, 1977. All dives were made between 1000 and 1700 hrs daily and served to familiarize the observers with both the study site and cunner social behaviour, as well as providing data on the behaviour of cunners between emergence from overwintering torpor and the establishment of territories. During this period, 10 territorial males

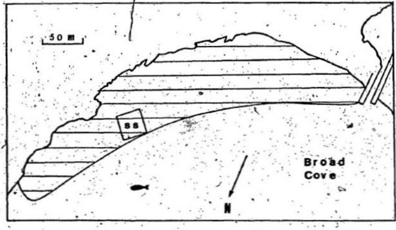


Figure 1. Map of Broad Cove, Conception Bay, showing location of the primary study site (SS) and the area searched for tagged fish (horizontally - lined area).

in the 210 - 260 mm (TL) range, were selected as subjects of an intensive study of territorial and reproductive behaviour. These were the first territorial individuals recognized, but were not necessarily the first to establish territories. All subjects were tagged (see below) and mapping of territories commenced.

Preliminary observations indicated that a 15 min observation period/fish would provide sufficient quantitative and qualitative data to characterize activity at any time of day. Quantitative data were obtained during 442 individual snorkel observations, each of 15 min duration, on the 10 tagged males. Fish were observed in random order and at random hours between 0600 and 2100 daily, on 31 arbitrarily selected days between 6 July and 23 August, 1977.

The number of cunners observed during a dive ranged from 4 - 10, and varied with sea state, water temperature (range: 9.0 - 16.5°C), and number of observers available. Water temperature was the principal limiting factor of dive duration.

During each observation occurrences of social interactions related to territorial and reproductive behaviour were tallied on slates and coded to designate interactions with contraspecifics, or conspecific males, females, or juveniles. A submersible event recorder console was used in 32 observations to provide data on duration of behavioural parameters. A suffixed code system identified fish involved in interactions with territorial males, as in the slate recordings. The console was connected to an Esterline Angus Series A event recorder, carried in a moored Zodiac, by a buoyed 30 m cable. Recorder chart speed was 7.6 cm per min providing a resolution of 2 sec per chart graduation.

Qualitative data obtained during observations were summarized at the conclusion of each dive and sightings of tagged females were recorded. Brief qualitative observations were made on females present during observations of territorial males. Periodically, the cove north of the Broad Cove River was searched to a depth of 10 m and the locations of tagged fish were recorded.

Additional observations on the behaviour of both males and females were made between May and September, 1978. Unless otherwise noted, all quantitative data presented in the figures and tables pertain to the 1977 observations.

Capture and tagging

Fish collected in 1977 for tagging, measurement, and/or sex determination by stripping were captured by SCUBA divers in dip nets baited with crushed sea urchins. All territorial males and 25 females tagged prior to July 17 were tagged and released immediately at capture depth. Lengths of territorial males were estimated visually. All other fish were measured and sexed at the surface before release.

Floy FD 67 'spaghetti' tags were inserted in the dorsal musculature below the mid-point of the dorsal fin. All tags were numbered and, with the exception of those used on 28 July, bore a distinctive colour code. Masking of colour codes by filamentous algae and colonial diatoms hindered identification of several females. If such a fish was seen during a series of observations an attempt to approach the fish and read the tag number was made only after completion of activity recording. (Preliminary dives had shown that the presence of a diver on the substrate could attract large numbers of cunners to a territory, resulting in an abnormally high level of social interaction.)

In 1978, all fish were captured in a baited 1 m diameter hoop net and brought to the surface for examination or tagging. Colour coded Floy FD 67 tags were inserted as described above.

There were no known tagging mortalities. Tagging did not visibly affect either swimming ability or social interactions. Tag losses were high; 80% of the territorial males tagged in 1977 had lost their tags within 5 weeks. As these fish were extremely difficult to recapture, only 3 were retagged. The use of a longer tagging needle in 1978 reduced tag loss among males to 17%.

Territory boundary determination and mapping

Territory boundaries were determined by surface observation of territorial cunners. Fluorescent orange floats 2.5 cm in diameter, attached to lead weights by 0.3 m of heavy twine, were used as boundary markers. These were placed at the sites of 'border disputes' between adjacent territorial fish. Disputes were of two types: a static mutual frontal display, and a lateral display which usually incorporated parallel swimming. Frequently, a section or sections of one territory did not adjoin another. In such cases markers were placed at the outer limits of normal cruising activity. If a territorial fish was completely surrounded by others, its cruising range was restricted to the area within the perimeter defined by border disputes.

The point at which a territorial fish terminated pursuit of an intruder was an unreliable indicator of boundary location. Many chases extended beyond the territory or ended before the fleeing fish had reached the perimeter. The distances between markers were determined by direct measurement, and through triangulation, a planar perimeter map of the 1977 territories was drawn.

Temporary removal of fish from the population

In an attempt to elicit foraging behaviour and, in the case of territorial fish, to determine the effect of temporary removal from the population on ability to reoccupy the territory, 3 pairs of tagged cunners were confined in a holding cage for periods of 5 - 7 days. The holding cage was located at a depth of 3.5 m (MLW) inshore of the primary study site. The cage was constructed of 19 mm mesh twine netting on a 30 X 90 X 60 cm high steel frame.

All 6 cunners were captured between 1300 and 1600 hrs and released between 1100 and 1400 hrs. The first 2 pairs, each composed of a territorial male and territorial female, were captured on 25 and 31 July and released after 5 and 7 days respectively. A nonterritorial male and female were caged from 7 - 14 August.

A diver opened a trap door in the holding cage to allow the occupants to escape. If a fish failed to leave within 2 - 3 min the cage was tipped to direct the occupant to the exit. Each subject was followed for at least 30 min after release or until lost to sight. Observers recorded the course followed by the fish, and time and locations of social interactions.

Plankton tows

Nine surface tows for ichthyoplankton were made during the 1977 spawning season. Each tow covered a marked 120 m course at a speed of 3 knots, over a depth range of 1 - 10 m, with a 120 mm diameter fine mesh net. A 240 mm diameter net was used for 9 tows during July and August, 1978.

Quantitative data analysis

Standard SPSS (Nie et al., 1975) programs for correlation and simple bivariate regression were used to test for relationships between behavioural parameters and independent variable (week, time of day, tidal phase, water temperature). G_H tests (Sokal and Rohlf, 1969) were used to test for correlations of T. adspersus reproductive behaviour with tidal phase, due to the low recorded frequencies of courtship approaches and spawns relative to total number of observations made. G_H tests were also used to analyze variation in frequency of other infrequently observed behaviours (daylight quiescence, foraging behaviour, absence from territory) with time of day and/or between subjects.

Two-way Model II anovas without replication (Sokal and Rohlf, 1969) were used to analyze variation in frequency of courtship approaches and spawns with time of day and between subjects. Data were obtained by repeated observations of 10 territorial males and for test purposes it was assumed that there was no interaction between time and these individuals.

RESULTS

General observations and behavioural parameters

A. Sex ratio and population structure

The Broad Cove cunner population is composed of juveniles, and adult territorial and nonterritorial fish of both sexes. Cunners with juvenile colouration are relatively scarce and are usually found in close proximity to shelter, particularly growths of *Agarum cribrosum*, the only common sublittoral macrophyte in the cove.

Territorial males are larger than the majority of females and nonterritorial males. The average TL of 14 territorial males captured in 1978 was 239 mm (range: 210 - 262 mm) as opposed to a mean TL of 207 mm (range: 165 - 260 mm, n = 28) for both territorial and nonterritorial fish taken in 1977, and a mean TL of 212 mm (range: 120 - 295 mm, n = 52) for all males captured in 1978. There was no distinction in size between territorial and nonterritorial females of >170 mm TL, the minumum recorded length for territorial cunners. The mean total lengths of females captured in 1977 and 1978 were 211 mm (range: 160 - 320 mm, n = 53) and 194 mm (range: 155 - 270 mm, n = 46) respectively. The relative numbers of territorial and nonterritorial fish in the population are unknown.

Age - length data for Broad Cove cunners (Naidu, 1966) indicate that the majority of territorial males are at least 7 years old, whereas the smallest territorial females are ~4 years of age. The mean age of 11 territorial males speared in 1978 was 9.2 years (range: 7 - 12 years) (D. Martin, personal communication).

Naidu (1966) reported a 1:2.8 male to female ratio for his Broad

Cove sample collected in July or August by hook and line, at a wharf in the outflow of the Broad Cove River. On 16 August 1977, 4 males and 8 females were caught at the same location. Yet a 1:1 sex ratio was obtained for 57 fish collected > 250 m from the wharf on 17 and 20 August. A sample of 70 cunners captured in the same location on 22 August and 1 September 1978 yielded a 1.3:1 male to female ratio. This did not differ significantly from an expected ratio of 1:1.

Although males forage almost exclusively within their territories during the spawning season, females and nonterritorial males can be attracted to bait in large numbers. Few, if any, territorial males are located in the brackish water near the wharf. If Naidu's collection was made during the spawning season, these factors could account for the observed preponderance of females. Naidu's age data indicates that the majority of fish in his sample were females and nonterritorial males. The oldest male captured was 7 years old and 97.3% were < 6 years of age.

B. Sexual dichromatism

The sex of immature cunners, and of sexually mature fish of < 100 mm TL cannot be determined by external examination. Young T. adspersus are a bright orange-copper colour, with a prominent black spot at the junction of the spinous and soft portions of the dorsal fin. Although both sexes may reach sexual maturity at 80 mm TL, juvenile colouration can be retained to 100 mm TL or more (Johansen, 1925), with the dorsal spot becoming less prominent and an associated overall dulling and darkening of the body.

Upon emergence from overwintering torpor, cunners of both sexes > 150 mm TL were predominantly dull medium brown with a light cast to the belly. Although there were exceptions, most females had less blue belly and head colouration than males. A few fish of both sexes in the 200 - 250 mm TL range were red-orange. The colouration of the majority corresponded to Johansen's (1925) brown phase.

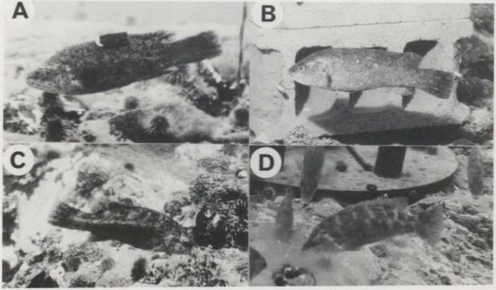
During the 4 - 5 week period before spawning commenced both territorial and nonterritorial males gradually acquired Johansen's blue phase colouration. The blue-white belly colouration became more widespread, with associated paling of the lower flanks. In some, but not all cases the lower half of the flanks developed a silvery sheen. The head was predominantly bright light blue, especially in the opercular and circumorbital regions (Figure 2A). The dorsal surface darkened to deep blue or purple. Potts (1974) cites a similar increase of blue colouration in spawning male <u>Crenilabrus</u> <u>melops</u>.

There was no change of female colouration in association with reproductive behaviour. The majority were brown phase (Figure 2B), many with very faint traces of 6 - 7 pale vertical bands, most distinct above the lateral line. Ripe females were easily recognized by their robustness.

A few strongly banded fish and individuals with pale lateral lines (Figure 2C) were seen throughout the study (i.e. May - November). Most were assumed to be female due to a lack of blue colouration, although it is possible that some males do not develop full nuptial colours. Figure 2D shows a cunner with distinct bands on the upper flank and caudal peduncle. Only one of 33 observed spawns involved a distinctly banded female; none of the spawning males were banded.

The banded phase in its full expression is analogous to that described by Dew (1976) after nocturnal observations of quiescent cunners, but is probably not an example of disruptive colouration. Banded fish were extremely conspicuous in mid-water aggregations and presumable more vul-

Figure 2. Patterns of colouration exhibited by adult *Tautogolabrus adspersus* in Newfoundland waters: A) male approximately one week after the spawning season; B) brown phase female; C) female with light brown lateral line and mottling on the head and upper flanks; D) female with distinct pale bands on the upper flanks and caudal peduncle. (Photographs B and D courtesy of Mr. H. Jacobs.)


A
B
C
D

nerable to predation.

The change from normal to banded phase is more probably associated with motivational state than with background. Removal of fish from water in both the field and laboratory could induce a pattern change in < 60 sec. No pattern change was observed in fish captured and released underwater. One of a pair of territorial males involved in an unusually long and intense agonistic interaction exhibited banded colouration. Potts (1974) reported a similar pattern change associated with both fright situations (i.e. capture by trawl) and prolonged agonistic encounters between territorial males in C. melops. Unlike the corkwing wrasse, T. adspersus does not lose its nuptial colours when a stress induced pattern change occurs. The banded cunners Dew (1976) found in the open at night may have been stressed due to a lack of shelter or by displacement from shelter by another fish.

C. Feeding behaviour

Although cunners feed both benthically and in the water column, territorial males were primarily bottom foragers during the spawning season. Loose aggregations of females and nonterritorial males were frequently seen feeding on plankton in mid-water in the manner described by Olla et al. (1975). Females foraged on the substrate either singly or in groups of 2 - 6 individuals.

Bottom foraging cunners moved slowly over the substrate, scanning it with pronounced eye movements. If prey was sighted the fish pitched forward at a sharp angle (50 - 90°) with the mouth just above bottom. In this position the fish is able to inspect potential prey with both eyes, possibly obtaining a more accurate fix on its location. The protrusible lips and strong teeth were used to remove prey from the substrate.

Large food items were torn apart by strong lateral movements of the head and entire body.

Field observations indicate that Ophiopholis aculeata, the daisy brittle star, is the principal benthic prey in Broad Cove. The territorial males studied in 1977 consumed 1 - 3 brittle stars in 27.5% of the observations in which foraging occurred.

The digestive tracts of two females collected for gonad examination contained 1 Nereis sp., 4 Tonicella rubra, 1 Mytilus edulis, 2 unidentified fish scales, >50 primary spines and interambulacral plate fragments of Strongylocentrotus droehbrachiensis, 1 intact arm and large numbers of calcareous skeletal components of O. aculeata. Stomach content analysis of ~ 400 cunners collected in Portugal Cove, Conception Bay, between May and September 1978, is in progress (D. Martin, personal communication). A sample of territorial males, speared in both Portugal and Broad Coves is also under examination to test for dietary differences between these fish and the general population.

Capelin, Mallotus villosus, appeared to be a major food source for cunners during late June and early July, 1977. Dozens of capelin which died during the spawning runs were strewn over the substrate for 2 - 3 weeks. In contrast, very few capelin appeared in the cove during 1978, fewer than six dead fish being seen in the study area.

Prior to the spawning season males could be lured from their territories with bait, although this became progressively more difficult with time. The 1977 sample males were rarely observed feeding outside of their territories during the spawning season. Male 22 left his territory and took part of a capelin from a nearby group of females, but returned before feeding. Males occasionally seized brittle stars from females foraging within their territories. Two fish were observed to turn over Asterias vulgaris, and they appeared to injest an object from the substrate beneath the starfish. After the spawning season males readily left their territories if bait was presented, or joined aggregations attracted by SCUBA divers. Territorial males fed or foraged in 10.9% of the 1977 observations. Significantly more foraging was observed before 1300 than after (Table 1).

Mid-water aggregations of nonterritorial males and females were attracted to bait from beyond visual range. On several occasions groups arrived en masse when bait was presented, or when lobsters attacked and devoured crabs. The main group was usually preceeded by a few solitary fish. Larger groups may be attracted initially by the movement of fish on their fringes toward food which the majority have not detected.

D. Location of nonterritorial fish

Nonterritorial cunners were most abundant in mid-water in the same locations as the aggregations formed after emergence from overwintering torpor. Loose aggregations of 10 - 30 fish were situated 5 - 10 m seaward of the study site on most days and appeared to reach maximum size in the early afternoon. Intrusions by females into males' territories were most frequent in late afternoon during the spawning season. At such times the mid-water groups were often reduced in size or absent.

Although aggregations included fish of both sexes, females usually outnumbered males by a ratio of at least 3:1. The male cunners in these groups were not observed to court females.

An attempt to observe the day to day behaviour of nonterritorial males provided little data. In late June and early July, 1978, 9 males of <230 mm TL ($\bar{X} = 205$ mm, range: 182 - 222 mm TL) and a larger num-

Table 1. Variation in frequency of foraging behaviour by territorial male *T. adspersus* with time of day.

Time of Day	Foraging during Observation	
	Yes	No
0600 - 1300	35	137
1300 - 2100	16	254

$G_H = 20.89$ df = 1

Foraging behaviour is not independent of time of day ($p < 0.005$).

ber of females were captured by hoop net. As all of the males were collected within the territories of previously tagged fish and were smaller than the average territorial male, they were assumed to be nonterritorial. All were tagged and released.

Subsequent observation showed one fish (215 mm TL) was territorial. Only three of the others were resighted. One male was seen in a mid-water aggregation on 17 July. Two weeks later, both this fish and another were observed in the same location, again in a group feeding on zooplankton. A third nonterritorial male was seen in an aggregation attracted to bait on 7 August.

E. Behavioural parameters

During field observations, occurrences of nine distinct actions related to territory defence and reproductive behaviour were recorded. Postures and movements associated with reproductive behaviour (courtship approach, circling, spawn) are described on pages 53 - 58. Actions associated with territorial behaviour are described below:

Approach

This action consists of a forward movement by one fish toward another on an interception course. A slow approach is executed in the labriform mode of propulsion; a medium approach in a combined labriform and carangiform mode; and a rapid approach in the carangiform mode alone. Dorsal and anal fins are adducted or partly erect.

Chase

The chase action is a high speed movement toward another fish moving rapidly away from the subject. Movement of both fish is in carangiform mode with quick, low amplitude caudal beats. Pectoral and pelvic fins are adducted and the caudal fin is spread. Other median fins may be adducted or partly erect.

Lateral display and parallel swimming

The lateral display is an action whereby a fish swimming in the labriform mode presents a flank to another fish at a distance of 25 - 75 cm. Median and pelvic fins are usually adducted. Parallel swimming accompanies most interactions in which both participants exhibit lateral displays simultaneously. The fish follow parallel courses, just above the substrate, for distances up to 3 m, with intermittent halts, course reversals, or shifts from labriform to low speed carangiform locomotion. Erection of mediam fins occurs only during unusually long interactions which involve other forms of agonistic behaviour.

Frontal display

The frontal display is a posture in which a fish faces an opponent at a distance of 4 - 30 cm. The body is straight and oriented at 180° to the longitudinal axis of the opponent. Median fins are adducted. Gaping is a frequent component of the display. Opercular flaring has been reported as an occasional component (J. M. Green, personal communication) but was not observed during the study. Movement associated with the posture is performed entirely by the pectoral fins and consists of short, low amplitude backward and forward oscillations or slow movement toward the opponent.

Gape

The gape is a frequent component of the spawn and frontal display and an occasional component of the courtship approach. The action consists of a marked distension of the jaws and protrusion of the lips, which exposes the prominent, conical teeth and white lining of the buccal cavity.

Bite

The bite is an action in which a fish closes its jaws on part of another, with or without infliction of visible tissue damage.

Melee

A melee consists of a number of actions, both postures and movement, which follow a predictable pattern. It is initiated by the slow labriform approach of one gaping and frontal displaying fish to another, or by mutual forward movement, which results in the juxtaposition of heads as in Figure 3. One fish makes a sharp lateral head movement which terminates with a strike or bite against the opponent's jaws. The opponent responds almost simultaneously with the same movement. In extreme cases both fish lock jaws for >1 sec. In a quick series of movements each fish circles one or more times about the other and exchanges one or more bites. A melee ends when the participants turn away from each other or assume frontal display posture.

The mean durations of the actions described above, with the exception of melee, are presented in Table 2.

Table 2. Durations of behaviours associated with territory defense and reproduction in T. adspersus.

Behaviour	Mean Duration (sec)	Range	S.D.	N
Approach	2.9	1 - 20	2.6	380
Chases	2.4	1 - 8	1.5	96
Lateral display	3.5	1 - 10	2.0	27
Frontal display	8.3	4 - 15	4.8	4
Gape	8.3	4 - 15	4.8	4
Courtship approach	3.2	1 - 10	1.8	72

Male territorial behaviour

A. Establishment of territories and duration of territorial behaviour

Active cunners were first observed in early May, 1977 and in mid-May, 1978 when water temperature reached 5 - 6°C. The fish appeared sluggish and, although attracted to bait, did not feed. No cunners were seen on days when water temperature was $<5°C$. In late May, 1977, large nonpolarized aggregations were located near two known overwintering sites. Observations were concentrated on a group of cunners located over a 10 m wide strip of loose rock substrate between the drop-off at the outer edge of the primary study area and the nearest overwintering site.

Initially the aggregation comprised ~ 40 fish of either sex, all >120 mm TL. The fish were either stationary or moved slowly over the substrate at heights of 0 - 3 m. The aggregation reached a maximum size of 60 - 70 fish on 31 May 1977. A maximum size of ~ 100 cunners was attained by the same date in 1978. Chases and bites were observed within the aggregation but were not associated with territory defense as the fish involved either remained within or returned to the group immediately after the interactions.

By early June, 1977 several solitary fish were located 10 - 30 m inshore of the main aggregation, and polarized groups of 2 - 3 fish were observed swimming throughout the inshore area. During the first week of June aggregation size decreased to 20 - 30 fish and chases within the group were more frequent. The numbers of solitary cunners and small groups inshore continued to increase. By 8 June frontal displays, lateral displays, and chases had been observed and it was clear that many solitary cunners were territorial. As quantitative data were not collected during preliminary observations, the frequency of agonistic interactions between adjacent territorial males cannot be compared with data obtained during the months of July and August.

At least 6 of the 10 males observed in 1977 had established territories by 7 June, and the others had been tagged or identified by mid-month. The blue colouration of male cunners was pronounced by 10 June and development of light flank colouration had begun by 21 June.

A possible attempt to establish a new territory was observed in July and August, 1977. A male cunner of approximately 220 mm TL was seen at the intersection of territories 7, 21, and 23 (Figure 4, p 29) on 11 July. Approaches and lateral displays by adjacent territorial males failed to displace the intruder immediately. However, an hour later it was absent. This fish, or one of similar size, was seen in the same location on 13 and 18 - 21 July. It had returned again by 25 July and remained on the boundary between the territories until at least 23 August.

Throughout this period the male was involved in agonistic interactions with all 3 adjacent territorial males, and its movements were restricted to an area of 1 - 2 m^2 of bare bedrock. Between interactions this cunner moved slowly back and forth over or rested upon the substrate. It was not observed to spawn and made only 2 recorded courtship approaches to females. This male was not seen in 1978.

Several male cunners tagged in 1977 reoccupied their old territories in 1978. Male 23 had returned by 30 May. No fish were seen between 30 May and 7 June, due to a drop in water temperature. On 7 June Male 23 was again on his territory and Male 11 was seen in the large aggregation to seaward. On the following day Males 11 and 26 were seen in their 1977 territories. Male 26 had lost its tag but was identified by a split caudal fin. Male 7, identified by a tag scar and a white spot on the right caudal peduncle, had reoccupied his territory by mid-June. All other territories mapped in 1977 were occupied in 1978. However, the resident males could not be positively identified due to tag losses and lack of distinguishing physical characteristics. Four territorial males identified in 1977 but not included in the sample group defended the same territories in 1978. Three of these fish were tagged and the fourth had a distinctive white patch between the eyes.

Males observed in 1977 continued to show territorial behaviour at least until late September, although intermittently seen off their territories with feeding aggregations following the spawning season. Five territories were still occupied on 5 October. Water temperature was 6.8°C. A few (4 - 6) fish were seen moving among the large boulders at the overwintering site closest to shore. Many more were found in crevices in the substrate. Approximately 20 cunners emerged from shelter when bait was presented but showed little inclination to feed. All fish moved in a sluggish manner.

On a daily basis, territorial males remained on their territories from 0600 or earlier until dusk, between 2000 and 2100 hrs. Attempts to follow territorial males to their nocturnal shelters were unsuccessful. The fish were quickly lost to sight under low light conditions, even with the assistance of underwater lights. Previous observations (Green, unpublished data) had shown that some males remained on their territories at night, although in a state of nocturnal quiescence.

Males left their territories for periods of 0.5 - > 15.0 min in 3.6% of the 442 observations made in 1977. In 9 of 16 cases the fish swam toward the nearest overwintering site and returned within 1 - 5 min.

The cause of these brief absences is not known. On two additional occasions males joined feeding aggregations on the substrate 8 - 10 m from their territories. There was significant between fish variation in frequency of absence from the territory (Table 3). Male 21's absences accounted for 56.3% of the total number observed. The territory occupied by this fish was of medium size (32.3 m^2) with a substrate consisting primarily of exposed bedrock.

B. The nature of the territory

Territories in Broad Cove were located at depths of 0.7 - 13.0 m (MLW). The shallowest were within 5 m of shore, subject to strong turbulence during heavy seas, and probably untenable under such conditions. The deepest territories were found near the outer limits of the bedrock and boulder strewn substrate. Below 13.0 m a level plain of sand extends seaward. T. adspersus may establish deeper territories in areas with suitable substrate, as they have been caught at depths up to 130 m (Leim and Scott, 1966).

The horizontal surface areas of 10 territories measured in 1977 ranged from 16.1 - 74.3 m^2 ($\overline{X} = 44.7\ m^2$) (Figure 4). The mean area of 4 territories measured during an earlier study was 18.6 m^2 (Green, unpublished). These were located at depths of 6 - 10 m on a substrate of loose rock rubble. There appeared to be no relationship between fish size and area of the territory occupied as some large males occupied small territories. Aggressive behaviour toward intruders, measured by the parameter Chase, was not correlated with territory size ($r = {}^{-}0.03$, $df = 9$, $p > 0.90$) (Table 4 A). It was expected that frequency of agonistic interactions with adjacent territorial fish would be more closely related to territory size than aggressive behaviour toward transient intruders.

Table 3. Variation in frequency of absence from territory between sample male _T. adspersus_.

Fish	Absent from Territory	
	Yes	No
7	0	44
8	0	45
11	0	44
17	1	44
19	3	43
21	9	35
22	1	42
23	0	44
25	0	43
26	2	41

$G_H = 102.72$ df = 9

There is significant between fish variation in frequency of absence from territory ($p < 0.005$).

Figure 4. Planar perimeter map of territories defended by the 10 male *T. adspersus* observed during the 1977 field study. Numbers within the territory boundaries represent the tag number of the resident male and the area of the territory in m^2.

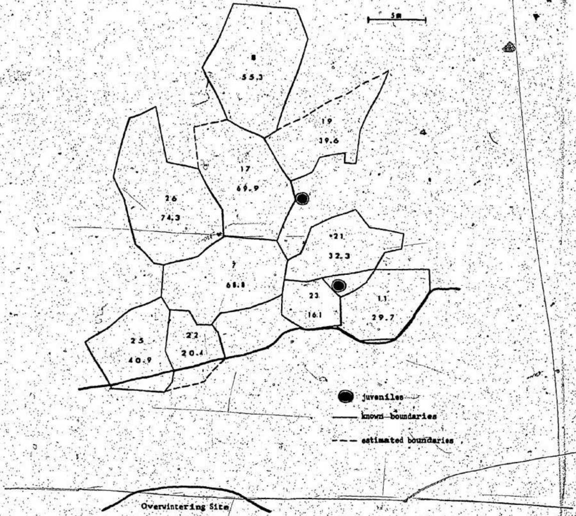

5m
8
55.3
19
39.6
17
69.9
26
74.3
21
32.3
7
68.8
23
16.1
11
29.7
25
40.9
22
20.4
juveniles
known boundaries
estimated boundaries
Overwintering Site

Table 4. Correlations of total number of chases (A), lateral displays (B), and frontal displays (C) performed by territorial male T. *adspersus* with area of territory defended.

A.

Fish	Chases	Area of Territory
7	191	68.8
8	85	55.3
11	135	29.7
17	146	69.9
19	97	39.6
21	61	32.3
22	123	20.4
23	210	16.1
25	135	40.9
26	115	74.3

$r = -0.03$ $t = -0.09$

No significant correlation between area of territory defended and number of chases performed ($p > 0.90$).

B.

Fish	Lateral Displays	Area of Territory
7	28	68.8
8	19	55.3
11	32	29.7
17	33	69.9
19	20	39.6
21	41	32.3
22	23	20.4
23	26	16.1
25	35	40.9
26	60	74.3

$r = +0.41$ $t = +1.27$

No significant correlation between area of territory defended and number of lateral displays performed ($p > 0.20$).

Table 4.

C.

Fish	Frontal Displays	Area of Territory
7	10	68.8
8	5	55.3
11	5	29.7
17	3	69.9
19	2	39.6
21	12	32.3
22	10	20.4
23	7	16.1
25	6	40.9
26	11	74.3

$r = -0.005$ $t = -0.01$

No significant correlation between area of territory defended and number of frontal displays performed ($p > 0.90$).

However, performance of neither lateral ($r = +0.41$, $df = 9$, $p > 0.20$) nor frontal ($r = -0.005$, $df = 9$, $p > 0.90$)displays was correlated with territory size (Table 4 B, C).

Territory boundaries corresponded to prominent topographic features such as bedrock ridges, edges of drop-offs, and large boulders. Most of these features were of sufficient height to visually isolate adjacent males, as cunners tend to remain close to the substrate. On relatively level expanses of substrate, territory boundaries extended from one small but prominent rock or outcrop to another. Border confrontations occurred almost exclusively on level ground, possible due to more frequent visual contact between territorial males.

The majority of territories contained a large boulder or bedrock outcrop near which the resident cunner was found when not patrolling or foraging. When disturbed by divers, cunners often utilized these features as shelter. Deep crevices may have substituted as a source of shelter in two other territories.

Territory boundaries appeared to be stable on a seasonal basis. However, the death of Male 17 in late September, 1977 resulted in size increases of at least two adjacent territories in the following spring (Male 17 had been speared by another diver). The central portion of Territory 17 appeared to have been occupied by another male. Territory 26 had decreased in size in 1978, while the boundaries of Territories 11 and 23 were unchanged.

C. Interactions with conspecific intruders

Following the establishment of territories in early May, intruders of either sex were chased. However, during the July to August spawning season territorial males were more likely to court than chase female intruders. Territories were actively patrolled, usually in an apparently random fashion, although some fish followed a predictable route when moving from one part of a territory to another. Responses to female cunners were variable. Although most were courted or chased others were 'ignored.' Included in the latter group were the territorial females present in several of the males' territories. These fish were chased and courted, but less frequently than were transient females. The behaviour of territorial females and their interactions with males are described below (p 42 - 43).

Nonterritorial males were always driven from territories by the resident males and did not exhibit agonistic behaviour toward them. On two occasions nonterritorial males which accidentally came upon a territorial male from behind turned and fled, although the latter apparently failed to see the intruders. Territorial males may be recognized by conspecifics by their large size and constant presence in a particular location on the substrate.

If bait was used to attract large numbers of intruders, including nonterritorial males, territorial fish tended to chase fish on the periphery of the feeding aggregation as well as late arrivals and departing individuals, and did not feed.

Interactions between adjacent territorial males were almost exclusively 'boundary disputes' in which lateral and frontal displays were performed. Males rarely intruded into other territories, and did so usually while chasing an intruder from their own. An intrusion by a territorial male, if detected, elicited an immediate approach by the resident fish. Unless the intruder was deep within the territory further interaction was unlikely. If the fish was slow to leave the territory and was chased by the resident, a border dispute often followed. More rarely, the males engaged in a series of short reciprocal chases across the boundary.

Lateral displays and parallel swimming were initiated most frequently by one territorial males approach to another near their common boundary. Long bouts of parallel swimming were succeeded by or interspersed with frontal displays. More rarely, frontal displays were followed by bites and melees.

Sequence diagrams of responses by territorial male T. adspersus to intruding females and nonterritorial males, and to intruding or nearby territorial males are presented in Figure 5.

D. Interactions with juveniles[1]

Fewer than 20 juvenile cunners were seen in the study area. Nearly all were located in the shallowest part of the site, where Agarum cribrosum was most abundant. The orange colouration of juveniles closely matches that of A. cribrosum. Johansen (1925) stated juveniles were usually the same colour as the predominant algal species in the habitat, and could occur in green, brown, or orange phases. Juveniles generally remained within 1 - 2 m of an algal growth or narrow crevice and took shelter in one or the other when threatened by divers or other cunners.

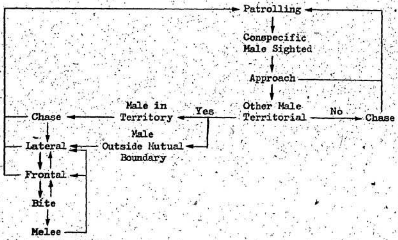
Territorial males did not consistently pursue juveniles, although the latter were almost always present above the substrate, apparently feeding on plankton. Males often passed close to juveniles without aggresive behaviour, the smaller fish either moving a short distance away or showing no reaction to the adult's presence. Several chases appeared to

---

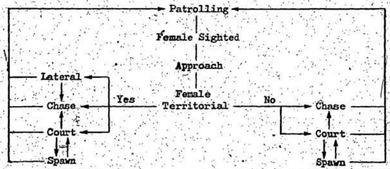
[1] The term juvenile, as used here, refers to colouration only; not to sexual maturity. Juvenile colouration is generally restricted to fish of <100 mm TL.

Figure 5. Sequence diagrams of interactions between territorial male *T. adspersus* and male (A) and female (B) conspecifics.

A.



B.



be initiated by the sudden flight of a juvenile from a slowly approaching male.

When chased, juveniles which failed to reach shelter immediately utilized their small size and greater manoeuverability to elude pursuit. Chases were restricted to a small area and, if long (i.e. > 3 sec), followed extremely convoluted paths, due to frequent horizontal and vertical turns by the smaller fish. Chases ended when the adult male ceased pursuit, often still within his territory or, more frequently, when the juvenile reached shelter. On three occasions, males made prolonged attempts (max 5 min) to reach juveniles in crevices or entered algal clumps used as shelter, only rarely forcing the smaller fish into the open. Sudden dashes at plants used as shelter occurred when juveniles were not visible to the observer.

Social interactions between females or nonterritorial males and juveniles were not observed. Several chases and a frontal display involving only juveniles were recorded. The principal areas occupied by juveniles (Figure 4, p 29) were either part of or immediately adjacent to the territories of Males 11, 17, 21, and 23. Consequently, these males initiated 87% ([illegible]/53) of the agonistic interactions with young fish recorded in 1977.

E. Interactions with contraspecific intruders

Territorial males were the only cunners observed in interactions with contraspecific icthyofauna. Males exhibited agonistic behaviour toward <u>Pholis gunnellus</u> (n = 16), <u>Pseudopleuronectes americanus</u> (n = 4), <u>Gadus morhua</u> (n = 1), and <u>Mallotus villosus</u> (n = 1) (n = number of chases recorded). Two winter flounder were bitten as they were driven from a territory. Although quantitative data are lacking, observations suggest Pholis gunnellus is the most abundant contraspecific in the area.

Male T. adspersus made 15 approaches to contraspecific intruders without subsequent contact, pursuit, or display. A large Anguilla rostrata, two P. americanus, and a Macrozoarces americanus were followed during transits of territories. A Myoxocephalus octodecemspinosus, two P. americanus, and two P. gunnellus, all initially resting on the substrate, slowly swam off when approached. Several approaches to flounders and sculpins, and one each to a cod and gunnel elicited no response. In these cases the cunner showed no further reaction to the intruders' presence.

Reactions of territorial T. adspersus to contraspecific intruders other than P. gunnellus were inconsistant. Though intrusions by flounder and various cottids were frequent, cunners rarely exhibited agonistic behaviour toward them. Rock gunnels were usually chased at high speed but never caught. Gunnels always attempted to reach shelter in the substrate or in Agarum cribrosum. Two gunnels were dislodged from their first shelters and chased again, one for 4 m beyond the territory.

Pholis gunnellus is probably not a prey species of the cunner. Both cunners and gunnels have been observed feeding together on crushed sea urchins. In addition, a gunnel which did not flee when approached by a male cunner was repeatedly nudged along the substrate for > 2 m until pushed from the territory.

There was no evidence of serial territoriality with respect to contraspecifics, as observed in Eupomacentrus planifrons (Pomacentridae) (Thresher, 1976a). A single boundary seemed to apply for all intruders, whether conspecifics or contraspecifics.

F. Daylight quiescence

Territorial male T. adspersus remained immobile on the substrate for periods of 0.5 - 15.0 min ($\overline{X} = 7.0$ min, $n = 24$) in 5.4% of the 1977 observations. G_H tests (Table 5) showed significant between fish variation in the occurrence of daylight quiescence.

Quiescent males were normally found in crevices beneath boulders, under rock overhangs, or partly concealed by Agarum cribrosum. Only two cunners were seen in exposed positions. One male remained immobile (for > 15 min) in shadow ~ 25 cm from an outcrop of bedrock. Another settled on the substrate and tilted to one side until propped against a rock at an angle of ~ 45°. After two minutes it resumed patrol of the territory.

The number of shelters used by quiescent fish ranged from 1 - 4 per territory. Males occasionally switched from one shelter to another or made complete circuits of their territories before becoming inactive again. Daylight quiescent was more frequent before 1300 than after (Table 6). The cause or function of this behaviour is not known.

Table 5. Between fish variation in exhibition of daylight quiescence by territorial male T. adspersus.

Fish	Quiescent during Observation	
	Yes	No
7	0	44
8	5	40
11	1	43
17	0	45
19	0	46
21	9	35
22	2	41
23	1	43
25	6	37
26	0	43

$G_H = 40.36$ $df = 9$

Between fish variation is significant ($p < 0.005$).

Table 6. Variation in frequency of daylight quiescence with time of day. Data for all fish have been combined.

Time of Day	Quiescent during Observation	
	Yes	No
0600–1300	14	158
1300–2100	10	260

$G_H = 3.87$ df = 1

There is significant variation in frequency of daylight quiescence with time of day ($p < 0.05$).

Female territorial behaviour

A. Evidence for female territoriality

By early August, 1977 it was apparent that one or more cunners with female colouration were almost continually present in some males' territories. In contrast to other brown phase cunners, these did not flee from the territories when approached by the resident males, and occasionally made rapid dashes at the males' flanks. Such fish generally restricted their movements to a few square meters of a male's territory and frequently chased other brown phase cunners.

Although one of these cunners was observed to spawn twice with the same territorial male, it was suspected that some of the others were either males which had failed to develop spawning colouration or females undergoing protogynous hemaphroditism, a phenomenon unreported in T. adspersus but not uncommon in the family Labridae (Robertson and Choat, 1974). However, none of these fish courted others with female colouration.

Evidence that most, it not all, of these cunners were females was obtained in late summer, 1977 and during the 1978 field observations. By early August of both years the majority of brown phase fish could not be sexed by stripping. However, sperm could be stripped from nearly all blue phase fish two weeks later. The gonads of two territorial brown phase cunners collected in August and September, 1977 appeared identical to spent ovaries. A third, tagged, fish collected on 10 August 1978 in the same area it had defended in 1977 released 10 - 20 eggs when speared. Dissection showed that this cunner was a nearly spent female. During the 1978 field observations 3 of 8 tagged, territorial, brown phase cunners were courted by males and two of these subsequently spawned.

B. Nature of the territory

As territorial females are difficult to distinguish, in a casual survey, from other females foraging in, traversing, or being courted in a male's territory, the location and identification of such fish was confined to the primary study site. As a result, the depth range over which females establish territories is unknown. A total of 14 territorial females were identified in 1977 and 1978, all at depths of 4 - 5 m (MLW). In 12 cases a large boulder (width > 75 cm) or prominent bedrock outcrop was included in the territory. Females generally remained within 1 m of such topographic features, venturing further away to forage or to drive off intruders. At least five territories contained a crevice to which the female retreated when threatened by a territorial male. All territories were either entirely or partly within that of a male, usually on or adjacent to its border. For reasons cited below, the size of female's territories was difficult to determine with accuracy. The majority appeared to cover 4 - 6 m^2.

Territorial females were absent from 5 of the 13 males' territories examined in 1977 and 1978. Two of the males' territories were considerably smaller than the others. The remaining three had level, uniform substrates of bedrock or loose stone, which provided little cover.

C. Interactions with conspecifics

Interactions between territorial females and nonterritorial males and juveniles were not observed. Territorial males moved freely through those parts of their territories occupied by females. As they did, females often made either a slow approach and performed a brief (< 2 sec) lateral display or a rapid approach toward the male's flank with an abrupt turn away just before contact. Accompanying or immediately after the turn, the fish made 1 - 2 exaggerated movements of the caudal fin, which threw the body into a distinct sigmoid curve. In this posture the female's head was oriented at an angle of 45 - 60° away from the male's.

Territorial males generally continued on course following a lateral display by a female. However, following a rapid approach and turn away, the male frequently turned toward and began to follow the female. In such cases the female accelerated and continued to move away from the male. Brief chases occasionally followed and distances covered rarely exceeded 3 m. Territorial females either sought shelter in the substrate when chased or retreated until the male ceased pursuit.

The responses of territorial females to male intruders are thought to be related to territory defense, rather than reproductive behaviour. Courtship never followed these interactions. The behaviours described above may allow territorial males to distinguish between transient nonterritorial females and individuals present in the territory on a regular basis. Territorial females were courted and chased less frequently than others. There were no distinctions between the reproductive behaviours of territorial and nonterritorial females. Although two fish spawned twice with the male in whose territory they resided, another female left her territory to spawn with a different male in a territory 7 m distant.

Nonterritorial females usually moved off when approached by a territorial fish. A fast approach by the latter, or failure of the intruder to leave the territory after an initial approach, was followed by a brief chase. Due to the small size of the territories most chases covered a distance of 2 - 3 m. Territorial females were frequently unable to exclude larger cunners from their territories. When approached, large females either failed to respond or turned and approached the territorial fish. In such cases the latter always retreated.

Interactions between territorial female cunners were infrequent as few shared mutual boundaries and territories were generally several meters apart. With one exception (p 47) agonistic encounters were restricted to brief laterals, or short chases when one fish entered another's territory. Due to the low frequency of interactions between these females and other territorial fish, the boundaries of their territories were difficult to determine with accuracy and no measurements of territory area were obtained.

D. Duration of territorial behaviour

Complete seasonal data on duration of territorial behaviour is available for one female only. This cunner, Female 156, had been tagged in 1973, otherwise its presence on the fringe of the primary study site would have gone unnoticed. First seen in early June 1977, it defended a territory in the same location until early September, and was subsequently observed in midwater aggregations. Female 156 occupied the same territory from 8 June 1978 until speared for gonad examination in August. Five other females had left their territories between 6 and 17 August 1977, from 8 - 27 days after detection. In 1978, 6 females tagged in late June and early July vacated their territories between 24 July and 14 August. Two females were still territorial on 14 August. Duration of territorial behaviour after initial detection ranged from 11 - 42 days.

On a daily basis, females occupied their territories from before 0600 until dusk. It is not known whether the fish remain in the territories at night or seek shelter elsewhere.

E. Movements of tagged females

Sightings of tagged females indicated that most remained within 25 m of the tagging sites during the spawning season although some ranged considerably further afterwards. Data suggest that 5 of 24 females tagged at the primary study site in 1977 were territorial (Table 7). These cunners were repeatedly seen in the same locations on the substrate, all within males' territories. Female 38, tagged in Territory 22 on 16 July, was located 70 m inshore from 22 July to 6 August.

Four females were found 70 - 140 m north of the tagging site during all 10 combined sightings from 28 July to 24 August. Two others were seen 100 m and 158 m south in late August.

In late July, 1977, 24 females, many spent or nearly so, were captured at a depth of 8 m, 10 m seaward of the study site. The fish were tagged to provide data on postulated inshore movements during the afternoon. Tags were not colour coded.

In 17 of 19 subsequent sightings between 3 August and 1 September, fish from this group were in midwater aggregations within 10 m of the tagging site. One female was located 100 m to the north and another was seen at the outer edge of the study site, in Territory 23. Another was seen in the same area in early June 1978.

Two females tagged in 1977 were territorial in 1978 but, due to thick growths of algae on the tags, could not be identified. One of these fish occupied the same area defended by Female 37 in 1977. Attempts to capture and identify this female were unsuccessful.

Table 7. Frequency of sightings of tagged female _T. adspersus_ and maximum recorded distances of fish from tagging sites.

Fish	Frequency of sightings	Time Span (days)	Max. Dist. (m)
4	0	0	—
10	1	30	25
12	5	38	20
13	2	31	25
14	4	57	20
16	12	72	25
18	5	76	25
35	0	0	—
36 *	19	31	25
37 *	33	73	25
38 *	16	20	70
39	3	31	50
40	2	73	8
41	4	44	140
42	1	73	70
43	7	40	73
44	2	23	140
45 *	16	38	158
46	0	0	—
47	4	26	12
48 *	31	44	13
49	4	38	73
50	0	0	—
51	6	75	90
53	3	38	100

* Fish thought to have been territorial on the basis of repeated sightings in the same location.

Temporary removal of cunners from the population

The first pair of cunners,plated in the holding cage were released on 30 July at 1230, after 5 days of confinement. Courses followed by each fish are plotted in Figure 6 A.

Male 104 moved ~ 10 m seaward but was driven back by males in territories A and C, and chased choreward by Male 111. The fish swam northeast, parallel to shore and reversed course after encountering another territorial male. It began to zig-zag, still moving parallel to shore, but turned seaward after passing a large outcrop, and followed a nearly straight course to Territory 7. Male 104 then turned, passed through Territories 7 and 103 and entered his own, chased over the last 3 m by Male 103.

Once in his territory, Male 104 turned on 103 and engaged in a long (~3 min) agonistic interaction on their mutual border. Frontal and lateral displays were interspersed with melees, bites and jaw-locks. Male 104 engaged in 3 similar but shorter (<1 min) interactions with Males 11 and G before a second encounter with 103. Male 104 and Male F performed lateral displays with parallel swimming. Females in the territory were courted or chased between interactions with males. Observation ceased at 1320.

Female 53 returned to her territory within 15 min, after passing through a number of males' territories without incident. A lengthy interaction with a neighbouring territorial female (68) followed her return. This was the only incident in which females performed frontal displays, gapes, and jaw-locks. Both females were engaged in another, or possibly the same, interaction 50 min later. Male 104 and Female 53 successfully reoccupied their territories.

Male 111 and Female 68 were released on 7 August at 1122. Courses followed are plotted in Figure 6 B. (The holding cage was in the centre of 111's territory.) Female 68 was immediately chased from territory 111 and passed through Territory C into 126. She was driven from Territory 126 into 26 and immediately turned toward her own. At 1124, 2 min after release, she was lost to sight due to poor visibility. At 1129 she was relocated in Territory 7. Chased by the resident male, female 68 fled into Territory 103. At 1130 she was again lost to sight, having moved seaward or entered a deep crevice in Territory 23. On August 10, she was seen under a rock overhang in the same location. She did not reoccupy her territory.

After chasing Female 68, Male 111 engaged Male A in a short agonistic interaction on their mutual boundary. A long interaction with Male C followed, and included frontal displays, parallel swimming, bites and melees. The interaction continued for at least 35 min. The opponents were engaged in an almost continuous repetition of parallel swim, turn, parallel swim, frontal with gape, parallel swim . . . Approximately 30% of the frontal displays were followed by a melee with bites and jaw-locks. Within 5 min of the start of the interaction, Male B was bitten by Male 111 and assumed a strongly banded colouration in <10 sec. An hour and a half after release both fish were gaping and parallel swimming in the same location. However, bites were less frequent. Only one was recorded in 5 min of observation. Male 111 reoccupied its territory.

Nonterritorial Male 133 and nonterritorial Female 45 were released on 14 August, 7 days after capture. Courses followed after release are plotted in Figure 6 C. Male 133 swam toward Territory 104, turned, and moved without incident through Territories 26, 7, 103, and 23. He disappeared among boulders at the overwintering site at 1455.

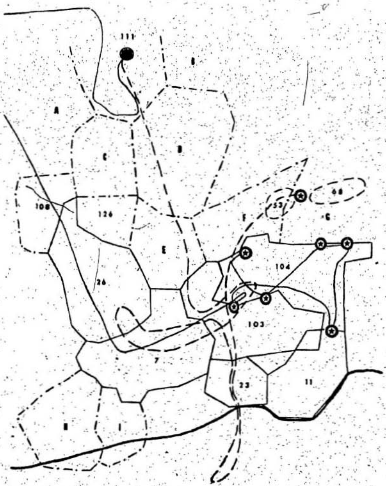
Female 45 entered Territory 126 and spawned with the resident male, 3 min after release. She then swam seaward through Territories 26 and 7, and remained at the base of a large boulder in Territory I for ~ 10 min. At 1450 she was seen moving seaward through Territory 23. At 1455 she was sighted in Territory 7, lost, and located again at the boulder in Territory I. Female 45 was last seen in this location at 1515. (In 1977, she was in Territories H and I in 8 of 20 sightings.)

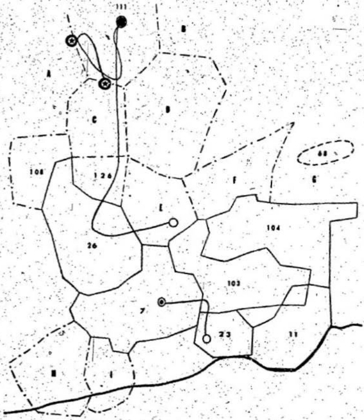
In summary, temporary removal of males from their territories did not impair their ability to reoccupy these areas upon release. Female 53 was also able to reoccupy her territory. All fish engaged in unusually long and intense interactions with their neighbours immediately after their return. Female 68's failure to return to her territory cannot be explained. She was probably capable of locating it. When lost to sight at 1124, she was within normal visual range of the territory and in the location where she was first captured and tagged.

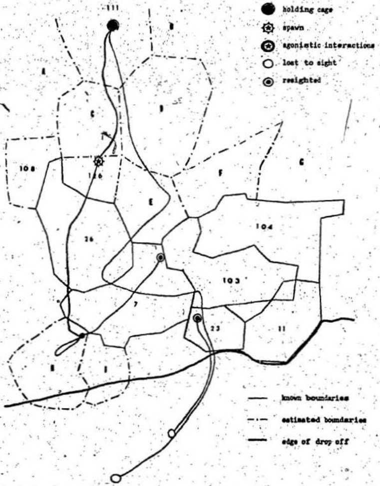
Although prevented from feeding, at least on benthic organisms, for periods of 5 - 7 days, none of the fish exhibited feeding or foraging behaviour upon release.

While the territorial males were confined, their neighbours gradually encroached upon those undefended areas adjacent to their own territories. The presence of Male 111, albeit caged, in the centre of his territory failed to discourage intrusions by Males A, B, C, and D. Neither of the vacated areas was occupied by a previously nonterritorial fish or completely partitioned between adjacent territorial males. 'Border disputes' between encroaching males were not observed.

Figure 6. Movements of cunners after release from the holding cage and locations of interactions with conspecifics: A) territorial male 104 and territorial female 53; B) territorial male 111 and territorial female 68; C) nonterritorial male 130 and nonterritorial female 45.


111
B
A
C
D
108
126
E
F
53
68
G
104
26
103
7
23
11
H
I


111
B
A
C
D
108
126
E
F
G
68
104
26
103
7
23
11
H
I


111
B
A
C
D
108
126
F
G
E
104
26
103
7
23
11
H
I
● holding cage
spawn
agonistic interactions
○ lost to sight
resighted
known boundaries
estimated boundaries
edge of drop off

Reproductive behaviour

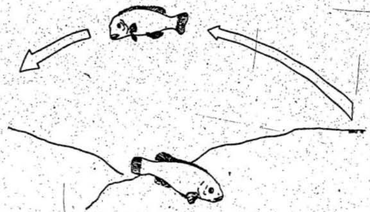
A. Courtship and spawning behaviour

Reproductive behaviour is initiated by a territorial male's 'courtship approach' (Figure 7) to a female within his territory. In this display the male swims toward and to one side of the female, with the bright blue median fins erect, and the head turned toward her at a sharp angle to the body. The belly is inclined slightly toward the female and locomotion is in the carangiform rather than the usual labriform mode, although rapid beating of the pectorals is a component of the display. In the vertical plane the male's course describes a shallow arch above the substrate to a maximum height of 1.5 m. The mean duration of 72 courtship approaches measured from activity recorder charts was 3.2 sec (S.D. = 1.8 sec; range: 1 - 10 sec).

Courtship behaviour was observed on 6 July 1977, 5 days before the first recorded spawn. Although initially described as occurring in the absence of intruders, it is possible that females immobile on the rocky substrate may have been overlooked. After the spawning season had begun females were present during all observed courtship approaches. In 1978 courtship behaviour was not seen until 14 July, 7 days before the first recorded spawn.

Nonterritorial females usually flee when approached by a courting male, the male often giving chase. It is uncertain whether these chases are attempts to drive the female away or to direct her back into the territory. Chases often end with the female still within its limits. If several females are present an almost continuous series of courtship approaches and chases can occur. Territorial females usually turn and move slowly away from a male if courted adjacent to the substrate, but

Figure 7. Courtship display by territorial male *T. adspersus*. The male has approached the nearly stationary female from ahead, curving slightly away and then back as he passes, with median fins erect and head turned sharply toward her.



are more likely to flee for cover when persistently courted in mid-water.

Receptive females rest on or move slowly over the substrate while the male makes one or more courtship approaches. If the female does not flee, the male usually begins to circle her at a height of < 1 m, either displaying on each side as in a courtship approach, displaying briefly while circling, swimming in a complete circle without raising the median fins or head turning, or holding the courtship approach posture during the entire circuit.

While the male circles, the female may make one or more short, slow forward movements along the substrate. Alternatively, she may either leave the territory, or move several meters while remaining within it. In the latter case, the male may resume courtship, again beginning with a courtship approach. After circling, the male slowly approaches the female from behind and passes over her several times (usually < 10) at an angle of 20 - 60° to her longitudinal axis, coming in contact with her dorsal surface and stiffly flexing his head and tail from side to side during some of the passes. During this phase of courtship the female may move forward again in a 'stop - start' fashion. The male then places his belly against her dorsal surface, with his snout just behird her head, and begins to quiver from snout to tail. In some spawns the slow body flexing is repeated. Within 5 - 15 seconds the pair begins to move forward and the male's quivering is transformed into slow, high amplititude, carangiform swimming, succeeded by rapid acceleration of both fish. Approximately 2 m from the starting point both make a sharp upward turn, with the female less than a body length ahead. (It is possible that the male nudges the female in the caudal region just before the turn. However, due to the rapidity of the transition from horizontal to nearly vertical swimming I cannot be certain of this).

The spawning pair rises at high speed at an angle of 60 - 80° to the substrate, with median fins erect, both gaping widely just before and during gamete release. Duration of the vertical run is ~ 1.5 sec. Spawning runs peaked 1.5 - 2.0 m above the substrate as both fish flexed sharply into a U-shape with their vents in close proximity. Randall and Randall (1963) have suggested that such flexion at the peak of vertical spawning runs, combined with a sudden expansion of the air bladder, " probably enhances the release of sex products." More recently, Robertson and Hoffman (1977) and Johannes (1978) have suggested that similar spawning runs in a variety of coral reef species may serve the dual function of releasing gametes far enough from the substrate to minimize reef-based egg predation, while only briefly exposing the spawning pair to predation away from the shelter of the reef.

Immediately after gamete release, the female folds her median fins and descends to the substrate, usually resting for a period ranging from several seconds to minutes, before leaving the territory. The male swims rapidly around the descending female in a wide, shallow spiral, again with median fins erect and head turned sharply toward her. The female may be chased for several meters if she swims off immediately after spawning. The patrolling of the territory and courtship of females is then resumed. On two occasions, females which have remained in the territory have spawned a second time within 5 minutes.

The duration of a full bout of reproductive behaviour, from courtship approach to spawn, ranges from 3 - 10 min, primarily in relation to the responses of the female. Termination of reproductive behaviour by departure of the female is most common during the approach and circling phase. Once the male is in direct contact with the female premature termination is rare. One female went through the entire courtship sequence four times before spawning. Each time the pair began the horizontal component of the spawning run, she turned under an overhanging rock face or entered a crevice, emerging after additional courtship displays by the male. Another female swam under a rock as the male began to quiver but did not emerge until he swam off. Courtship can be interrupted or even terminated by the presence of other fish. In one case a female left a territory after the resident male had repeatedly interrupted courtship to chase intruders during both the circling and quivering phases.

An atypical spawn followed two long chases (~ 8 sec each) involving a territorial male and an unusually small female (120 - 130 mm TL). After fleeing (or leading) back and forth over the territory at a height of 1.5 - 2.0 m, the female initiated an upward dash which ended in an apparently normal gamete release. Another spawn followed a short (<3 sec) mid-water chase of a female which occupied a territory on the edge of the male's. The female had fled after a single courtship approach by the male. Similar pair spawns, lacking specialized courtship displays, have been reported as normal for four species of <u>Halichoeres</u> (Roede, 1972).

B. Interference by males in pair spawning

Nonterritorial males with nuptial colouration were often seen in mid-water, several meters seaward of the drop-off at the outer edge of the primary study site, and were frequently chased by males occupying the outermost territories. Individuals from this group attempted to join the vertical runs of spawning pairs during 2 of 33 (5.9%) recorded spawns. Only one attempt was successful. The intruder had been chased repeatedly from the edge of the territory during courtship, but returned each time the male rejoined the female. In the other attempt the intruder was not seen before the spawn occurred. It arrived at high speed, moments too late to spawn, and immediately fled as the resident male approached. Similar interference by nonterritorial or subordinate males have been observed in Thalassoma bifasciatum (Warner et al., 1977) and Tautoga onitis (Olla et al., 1977) respectively. Territorial male T. adspersus used similar tactics to spawn with courting pairs near their territorial boundaries on two occasions. In 1978 a cunner with juvenile colouration attempted to intercept a spawning pair. It reached the peak of the run 20 cm behind the larger cunners and made the sharp flexion associated with gamete release at the same point that they had. The 'juvenile' immediately left the territory at high speed, although apparently not seen by the resident male until several meters distant.

Nonterritorial males occasionally tried to court females in a territory while the resident male was courting or chasing other intruders. All were quickly driven off. Due to poor visibility, the colouration of intruders approached or chased by territorial males could be determined in only 2055 of > 5000 recorded interactions (courtship approaches excluded). Only 5.8% of these interactions involved nonterritorial blue phase cunners. (All territorial males in the immediate vicinity of the 10 sample territories were either tagged or could be recognized by size, colour or location. Hence, there was negligible confusion between territorial and nonterritorial male intruders.)

C. Diurnal periodicity of sexual activity

i) Correlation with time of day

Courtship approaches were not tallied prior to 19 July, 1977 although first recorded 13 days earlier. After this date 88.7% were observed after

1300. Similarly, in 1978, 84.8% of recorded courtship approaches occurred after 1300. Frequency of courtship approach varied significantly with time of day (Table 8). Courtship was most intense between 1400 and 1900 hrs in 1977 and between 1300 and 1800 hrs in 1978 (Figure 8).

The earliest spawn was recorded at 1345; the latest at 2040. Spawning frequency varied with time of day (Table 9) and appeared to reach a peak between 1700 and 1900 (Figure 9 A). However, 1978 data showed a less defined peak (Figure 9 B).

ii) Correlation with tidal cycle

The tidal cycle was divided into four phases to test for correlations with cunner reproductive behaviour:

Phase 1 - high tide to mid-ebb
Phase 2 - mid-ebb to low tide
Phase 3 - low tide to mid-flood
Phase 4 - mid-flood to high tide

G_H tests (Sokal and Rohlf, 1969) were selected for the analyses due to the low numbers of recorded courtship approaches and spawns relative to the number of observations made. Data collected in 1978 could not be used as nearly all post-1300 observations were made during tidal phases 3 and 4. Frequency of courtship approaches did not vary significantly with tidal phase (Table 10 A). However, there was significant variation of spawning frequency (Table 10 B). Of the observations in which spawns were recorded, 64.5% (20/31) were made between mid-flood and high tide.

Spawning frequency and seasonality

The ten sample males and an additional tagged territorial male spawned from 1 - 7 times each ($\overline{X}$ = 3.0 spawns/fish/season) during the 1977

Table 8. Two-way anova of courtship approaches by sample male *T. adspersus* and by time of day. Frequency of courtship approach behaviour varies with time of day. Between fish variation of courtship approach behaviour is not significant.

	Time of Day						
Fish	0600-0900	0900-1100	1100-1300	1300-1500	1500-1700	1700-1900	1900-2100
7	0	1	3	17	52	3	0
8	1	0	2	13	5	4	0
11	0	1	2	6	4	43	4
17	4	1	3	21	10	3	0
19	0	0	8	12	1	1	0
21	1	1	0	0	0	2	0
22	0	0	1	2	7	9	13
23	0	0	0	6	9	24	1
25	0	0	3	5	5	7	0
26	1	0	7	9	6	5	3
	7	4	29	91	99	101	21

Source of Variation	df	F value	p
Columns (Time)	6	2.92	0.025
Row (Fish)	9	0.91	0.50
Error	54		

Table 9. Two-way anova of spawning by sample male <u>T. adspersus</u> and by time of day. Frequency of spawning varies with time of day. Between fish variation of spawning frequency is not significant.

Fish	Time of Day 1300-1500	 1500-1700	 1700-1900	 1900-2100
7	1	2	2	2
8	0	1	0	0
11	0	0	4	1
17	1	0	1	0
19	0	0	0	1
21	1	0	1	0
22	0	1	1	0
23	0	0	1	1
25	0	1	2	0
26	1	0	2	0
	4	5	14	5

Source of Variation	df	F value	p
Columns (Time)	3	4.09	0.025
Rows (Fish)	9	1.54	0.10
Error	27		

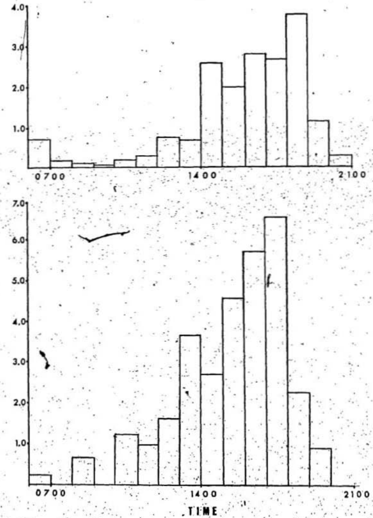


Figure 8. Hourly variation in frequency of courtship approaches by territorial male T. adspersus in 1977 (A) and 1978 (B). Vertical axes represent mean number of courtship approaches recorded per observation.

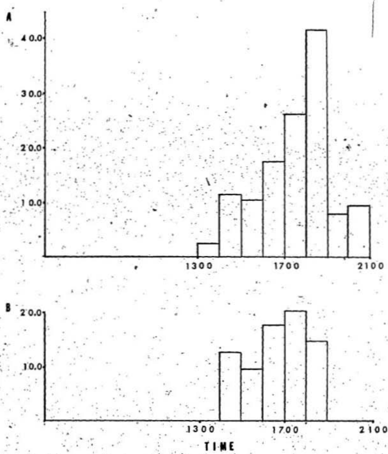


Figure 9. Hourly variation in frequency of spawns by territorial male T. adspersus in 1977 (A) and 1978 (B). Vertical axes represent the percentage of observations in which one or more spawns were recorded.

Table 10. Variation in frequency of T. adspersus reproductive behaviour with tidal phase (see p.59). Numbers in the 'Yes' columns represent the number of observations per tidal phase in which one or more courtship approaches (A) or spawns (B) were recorded. Only observations made after 1300 hrs are included in B.

A.

Tidal Phase	Courtship Approach Observed	
	Yes	No
1	15	32
2	29	38
3	24	55
4	20	56

$G_H = 4.94$ df = 3

Frequency of courtship approach behaviour is independent of tidal phase ($p > 0.10$).

B.

Tidal Phase	Spawn Observed	
	Yes	No
1	4	33
2	3	52
3	4	44
4	20	53

$G_H = 14.85$ df = 3

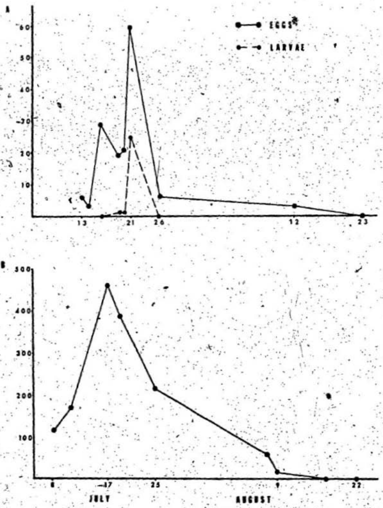
Spawning frequency is not independent of tidal phase ($p < 0.005$).

observations. There was no significant difference between sample fish in either the number of courtship approaches (Table 8) or spawns (Table 9) performed. Both males and females are able to spawn more than once/day on more than one day of the season. Three of the territorial males spawned twice within 15 min, while a fourth spawned three times in 6 min, twice with the same female. During 1977 a female spawned with the same male on 28 July and 9 August. In 1978 another spawned with a territorial male on 30 July and 3 August. In both cases the females were territorial within the area defended by their spawning partner.

The first spawn of the 1977 season was recorded on 11 July, the last on 9 August. No courtship behaviour was observed after 12 August. Most of 21 females tagged on 28 July were nearly spent, eggs being stripped from them with difficulty. At least 10 spent females were discarded during the tagging operation. Twelve fish collected on 16 August were examined in conjunction with a study on cunner enzyme (AHH) activity. One of 4 males and 7 of 8 females were spent (D. Walton, personal communication). Only 25 of 57 fish captured on 17 and 20 August, and released after external examination, could be sexed by stripping. All of these were males and, with the exception of a tagged territorial fish, were nearly spent. Four of the remaining fish were identified as spent males by colouration. In 1978 the first spawn was recorded on 14 July, the last on 14 August.

Surface tow results for 1977 (Figure 10 A) show a peak in the numbers of planktonic eggs and larvae on 21 July, and a sharp decline in numbers by 26 July. Only 3 eggs were collected on 12 August, and neither eggs nor larvae were present in the 23 August sample. Surface tow results for 1978 (Figure 10 B) again show a strong peak in egg number, which occurs on 17 July, followed by a gradual decline until the end of the spawning season in mid-August. Only 4 larvae were collected, 3 on 9 August and 1 on 17 August.

Figure 10. Results of plankton tows for T. adspersus eggs and larvae at Broad Cove, Conception Bay, in July and August 1977 (A) and 1978 (B). Vertical axes represent the numbers of eggs and larvae collected per tow. Only four larvae were obtained in 1978.


A
60
50
40
30
20
10
EGGS
LARVAE
13
21
26
12
23
B
500
400
300
200
100
8
17
25
9
22
JULY
AUGUST

Quantitative data

A. Correlations between behavioural parameters

The correlation coefficients between the behavioural parameters Approach, Chase, Lateral, Frontal, Courtship Approach, and Spawn, and their statistical significance are presented in Table 11. Sample size (n) for the parameter Courtship Approach was 299 observations as this behaviour was not recorded during the first 13 days of data collection. Only post-1300 observations (n = 270) were used in computation of correlation coefficients between Spawn and other parameters. Sample size for the remaining parameters was 442 observations. The covariants of each parameter are listed in descending order of significance in Table 12.

B. Diurnal periodicity of behavioural parameters

i) Variation with time of day

Anovas indicated that the recorded frequencies of the parameters Chase, Frontal, and Lateral did not vary significantly with hour of observation from 0600 - 2100. However, there was significant hourly variation of frequency of Approach, Spawn, and Courtship Approach behaviour (Table 13). Graphs of mean frequency/observation/hour suggested a peak in activity between 1800 and 1900 for all 3 parameters (Figures 8, 9, 11). Regressions and correlations of the parameters with time of day were performed with 2 groups of data; one of pre-1900 observations and the other of post-1800 observations, thus bracketing the period in which the graphed peaks occurred. Approach, Courtship Approach, and Spawn were positively correlated with time before 1900. Approach and Spawn were negatively correlated with time after 1800. With the exception of post-1800 Courtship Approaches, the parameters varied significantly with hour.

Table 11. Results of computer computation of correlations between behavioural parameters. Correlation coefficients and degrees of freedom are presented in the lower half of the table. The significance (p) of the correlations is presented in the upper half of the table.

	Approach	Chase	Lateral	Frontal	Courtship	Spawn
Approach		0.01	0.10	0.01	0.01	0.01
Chase	+0.53 (440)		0.20	0.20	0.01	0.50
Lateral	+0.07 (440)	-0.04 (440)		0.01	0.40	0.40
Frontal	+0.16 (440)	-0.05 (440)	+0.33 (440)		0.20	0.05
Courtship	+0.64 (297)	+0.17 (297)	-0.04 (297)	+0.06 (297)		0.01
Spawn	+0.35 (268)	+0.04 (268)	+0.05 (268)	+0.15 (268)	+0.34 (268)	

Table 12. Covariants of behavioural parameters. Covariants are listed in descending order of r value magnitude. All correlations are positive.

Parameters	Covariants
Approach	Courtship approach, Chase, Spawn, Lateral
Chase	Approach, Courtship approach
Lateral	Frontal
Frontal	Lateral, Approach, Spawn
Courtship approach	Approach, Spawn, Chase
Spawn	Approach, Courtship approach, Frontal

Table 13. Results of simple bivariate regressions of behavioural parameters on time of day.

			Time			
		0600-1900			1800-2100	
Parameters	df	F value	p	df	F value	p
Approach	1 376	58.65	0.001	1 79	15.98	0.001
Chase	1 376	4.44	0.05	1 79	0.01	0.75
Lateral display	1 376	0.66	0.25	1 79	0.01	0.75
Frontal display	1 376	4.64	0.05	1 79	1.25	0.25
Courtship approach	1 265	26.51	0.001	1 35	0.47	0.50
		1300-1900				
Spawn	1 205	14.57	0.001	1 79	12.06	0.001

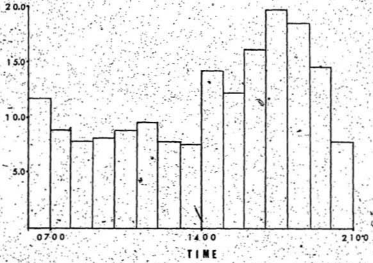


Figure 11. Hourly variation in frequency of approaches to conspecifics by territorial male T. adspersus. Vertical axis represents mean number of approaches recorded per observation.

ii) Variation with tidal phase

Regressions indicated that the parameters Spawn and Approach varied with tidal phase. The relationship between spawning and tidal phase has been described above. Both approaches and spawns were most frequent between mid-flood and high tides (i.e. tidal phase 4) (Figure 12).

C. Seasonal and temperature-related variation of behavioural parameters

Simple bivariate regressions showed significant variation of the parameters Approach and Chase with water temperature (Table 14). None of the other behavioural parameters varied with temperature during the July - August, 1977 observations.

The parameters Chase, Frontal, Lateral, and Courtship Approach varied with week of observation, measured from the start of regular observations on 6 July 1977. Performance of frontal displays, lateral displays, and courtship approaches was negatively correlated with week, whereas performance of chases was positively correlated with week of observation. The weekly variation in mean frequency of frontal displays, lateral displays, and courtship approaches per observation is plotted in Figure 13. The weekly variation in mean frequency of chases/observation and in mean temperature/observation is plotted in Figure 14. Although the graph shows an overall increase in chase behaviour with time, chase behaviour appears to be influenced more strongly by temperature than week, as confirmed by SPSS regressions (Table 15).

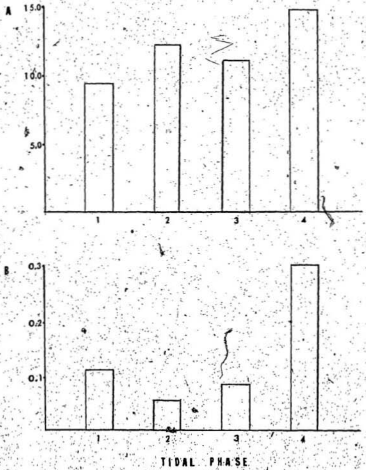


Figure 12. Variation of behavioural parameters with tidal phase (see p. 59). Vertical axes represent mean number of (A) approaches and (B) spawns recorded per observation.

Table 14. Results of simple bivariate regressions of behavioural parameters on temperature (C^{o}).

Parameter	df	F value	p
Approach	1 359	46.31	0.001
Chase	1 359	38.43	0.001
Lateral display	1 359	1.03	0.50
Frontal display	1 359	1.66	0.25
Courtship approach	1 234	1.78	0.25
Spawn	1 215	1.68	0.25

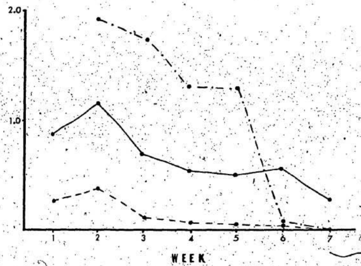


Figure 13. Weekly variation in frequency of courtship approaches (—·—·—), lateral displays (· ·), and frontal displays (——) by territorial male *T. adspersus* (6 July - 23 August 1977). Vertical axis represents mean number of each behavioural parameter recorded per observation.

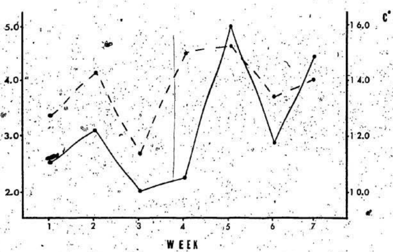


Figure 14. Weekly variation in temperature (C°) (----) and in frequency of chase behaviour (• •) by territorial male *T. adspersus*. Left vertical axis represents the mean number of chases recorded / observation / week.

Table 15. Results of simple bivariate regressions of behavioural parameters on week of observation.

Parameter	df	F value	p
Approach	1 440	2.26	0.10
Chase	1 440	18.26	0.001
Lateral display	1 440	13.79	0.001
Frontal display	1 440	37.37	0.001
Courtship approach	1 297	5.26	0.025
Spawn	1 268	2.26	0.10

DISCUSSION

Field observations of territorial male Tautogolabrus adspersus indicate that the spawning season in Conception Bay Newfoundland spans a 4 - 6 week period from early July to mid-August. This coincides with the period Reid (1929) concluded, on the basis of ichthyoplankton data, was " most favourable" for development of cunner eggs and larvae in the Gulf of St. Lawrence. In the Woods Hole region and off Connecticut, the cunner spawns in June and early July (Kuntz and Radcliffe, 1918; Costello et al., 1957; Dew, 1976). Cunners off Connecticut become active by mid-April at a water temperature of 5 - 6°C (Dew, 1976). Our data indicate that cunners in Conception Bay are inactive until the same temperature is reached, usually after mid-May. If, throughout the range of the species, a similar period is required to bring cunners to spawning condition after emergence from overwintering torpor, the later spawning season in the northern region may be due to later warming of the waters.

Reid's seasonal data showed a marked peak in egg abundance from mid- to late July. Abundance of eggs in Broad Cove peaked in the third week of July in both 1977 and 1978. Surface tow results, the significant decrease in courtship activity after mid-July, and the large proportion of spent females among those taken from late July onwards suggest that most spawns occur during the first 2 - 3 weeks of the spawning season. Although recorded spawning frequency did not vary significantly with week during the season, it is felt that a decrease in frequency as the season progresses cannot be ruled out due to the low power of the statistical tests.

The relationship between spawning and tidal phase is difficult to account for. Tidal effects on dispersal would be minor in Conception Bay due to low tidal amplitude (~ 1 m), but could be considerable in other parts of the species' range. Maximum offshore dispersal would be obtained if spawning occurred at high tide. Fish which spawned at low tide would achieve minimum offshore egg dispersal and, if in shallow water, would risk having eggs washed ashore. If maximum dispersal was the objective, spawning would be expected in approximately equal frequencies in the later part of the mid-flood to high tide phase and in the early part of the high tide to mid-ebb phase. However, this does not appear to be the case as most spawns were observed between mid-flood and high tide.

Whatever the cause of the quantitative relationship between tide and spawning frequency, time is the more important factor in the regulation of reproductive behaviour. Spawning is observed only after 1300 hrs and, although most frequent before high tide, can occur during any phase of the cycle. Late morning or afternoon spawning appears to be characteristic of labrid fish. There are clear advantages, in terms of reduced predation pressure, to not spawn in the early morning or late evening in coral reef habitats (Hobson, 1965, 1972). Field observations of territorial male T. adspersus indicate that the increase in approach behaviour after 1300 hrs is largely due to an influx of female intruders. Data on foraging frequency suggests that cunners devote the morning to feeding and the afternoon primarily to reproductive activity during the spawning season.

T. adspersus pair spawning is generally similar to that of other labrid species. The vertical spawning run is a common feature of reproductive behaviour among both labrids and scarids with pelagic eggs. Male T. adspersus, Duymaeria flagellifera (Nakazono and Tsukahara, 1974), *Crenilabrus melops* (Potts, 1974), *Clepticus parrae* (Robertson and Hoffman, 1977), *T. onitis* (Olla and Samet, 1977; Olla et al., 1977), and *T. bifasciatum* (Reinboth, 1973) are all aggressive toward other males during the spawning season. The first three species defend territories, whereas the last three attempt to exclude males from a less distinct spawning site or sites.

Prior to the spawning season males of *T. adspersus*, *T. onitis*, and *C. melops* exhibit aggressive behaviour to conspecifics of both sexes, usually initiated by a high speed approach to intruders. This approach, modified in the cunner, tautog, and corkwing wrasse, subsequently becomes a component of courtship. Circling of a receptive female or both circling and rapid passes to the side, with exaggerated swimming movements, are components of courtship in these species and in *Labroides phthirophagus* (Youngbluth, 1968), *Crenilabrus temminckii* (Moyer and Shepard, 1975), *D. flagellifera* (Nakazono and Tsukahara, 1974), and pair spawning *T. bifasciatum* (Reinboth, 1973) and *T. cupido* (Meyer, 1977). Like the cunner, *L. phthirophagus* faces the female during courtship displays and leans the dorsal surface away. Similar tilting by *T. adspersus* may enhance the display through presentation of the bright belly and flank. Alternatively, leaning may counteract a tendency to roll while the male's head is turned toward the female.

Female cunners do not communicate receptivity to courtship by any visible means other than relative immobility on the substrate and failure to flee as a male approaches.

Pair spawning has been described for a number of labrid species; Moyer and Shepard (1975), Nakazono and Tsukahara (1974), Olla and Samet (1977), Potts (1974), Randall and Randall (1963), Reinboth

(1973), Robertson and Choat (1974), Roede (1972), Youngbluth (1968). At least two species, *Thalassoma bifasciatum* and *T. lunare* exhibit dualistic reproductive behaviour. Roede (1972) described what may have been group spawning *Halichoeres bivittatus* and *H. maculipima*, species previously thought to be exclusively pair spawners.

Group spawning by *Tautogolabrus adspersus* has been recorded only in American waters and pair spawning only in Newfoundland. It might seem that these dualistic reproductive behaviours are mutually exclusive in parts of the cunner's range. However, a number of factors indicate such a conclusion is premature.

The group spawning cunners described by Wicklund (1970) were of a size at which sexual dichromatism is poorly developed or lacking in Newfoundland waters. The larger cunners present defended territories but were not observed to spawn. The active "defense" of these territories may have included courtship approaches to females. To the casual observer, these could easily be misinterpreted as agonistic behaviour, as females usually flee when approached. The low frequency of pair spawning (0.3 spawns/hour of observation in the present study) may explain why it was not observed. The non-participation of large, territorial fish in group spawning is consistent with descriptions of dualistic reproductive behaviour in other labrid species.

Although group spawning by *T. adspersus* has not been seen in Newfoundland, the possibility of its occurrence cannot be discounted. The mean TL of fish taken in the present study was 211 m. Fish of less than 125 mm TL (i.e. those which group spawn in southern waters) were scarce. However, collections on the southwest coast of Newfoundland in 1968 and 1970 consisted mainly of fish of this size of smaller, some with mature gonads (Green, unpublished data). Although several dives were made in the area in 1978, group spawns were not observed. Again this may be a consequence of limited observation time and infrequent spawning. Too little is known with regard to the behaviour of young cunners to explain their low numbers at Broad Cove, or to suggest why they might be more plentiful in other locations.

Robertson and Choat (1974) suggested that group spawning in labrids could arise when small, drab, sexually mature males were able to collectively over-ride female mate choice for older, more colourful males or 'gaudies.' Under normal conditions young males would be largely unrecognizable to females as potential males, due to their similar colouration. If young males exhibited courtship behaviour near territorial males they might risk recognition and attack and the female could still select the gaudy male over the drab. Robertson and Choat suggest that the solution is the formation of aggregations in which drab males heavily outnumber females. "Because these large concentrations tend to be away from gaudies' territories, the probability of a direct choice situation arising is reduced. When a choice does arise it is of many drabs against perhaps a single gaudy, which would help reduce the relative stimulus value of the gaudy."[2] The stimulation provided by many drab males clustering about a female would then be sufficient to elicit a spawn.

This being the case, it is curious that the nonterritorial males in Broad Cove have not been observed to group spawn. Most nonterritorial males are of a size at which sexual dichromatism is well developed. Presumably an aggregation of 'gaudy' males would be more stimulating to a female than one of drab males. Lack of group spawning may be related

---

[2] Robertson and Choat (1974) p. 224

to the low numbers of males in mid-water aggregations. Without data on the relative numbers of territorial and nonterritorial cunners in the population and the relative abundance of different age classes, the apparent lack of group spawning in Broad Cove cannot be explained.

Only territorial male T. adspersus were observed to successfully court and spawn with females. This suggests that sexual activity is largely restricted to females and to the older and larger males. Thus, the sex ratio of the breeding population must differ from the observed 1:1 ratio of the general population. Similar discrepancies in sex ratio of the breeding and general populations have been recorded in other promiscuous and polygynous bird and fish species (Noble, 1938; Randall and Randall, 1963; Selander, 1965).

Although spawning is almost exclusively performed by territorial males of at least 7 years of age, Johansen's data (1925) and the observed attempts of 'juveniles' and nonterritorial males to join spawning pairs indicate that the sexual maturation of male T. adspersus is not delayed. In a situation where males defend the same territory from year to year and are capable of maintaining relatively inflexible boundaries, some fish may never obtain a territory. Natural selection would favour the expenditure of energy by young and/or nonterritorial fish in gonadal development, in case an opportunity to join pair spawners arose. It is of interest to note that nonterritorial male T. adspersus were most frequently seen in mid-water, seaward of the territories along the edge of the drop off from 4 - 6.5 m, and that the observed attempts to join spawning fish occurred in these territories alone. It is probably easier to gain access to fringe territories such as these than to territories in more central locations.

With such a high premium, in terms of reproductive fitness, associated with male territoriality, intense competition for territories would be expected in late May and early June, when territories are reoccupied by previously territorial fish, and when competition for areas vacated due to overwintering mortality would be expected. Although not recorded, such competition may occur, as relatively few observations have been made in May and June. No quantitative data are available for comparison of frequency of aggression toward conspecifics during territory establishment with frequency later in the season.

Territorial behaviour in reef and other benthic fish can have several functions defense of spawn, shelter, and/or a food resource. The cunner's pelagic eggs and larvae preclude defense of spawn. Territorial behaviour in male T. adspersus does entail maintenance of an exclusive spawning area, and this may be its primary function. A number of data support this viewpoint: the consistent agonistic responses to male intruders as opposed to tolerance of receptive females within the territory, the concurrent decrease of courtship behaviour and aggressive interactions between territorial males, and the more frequent forays outside the territory after spawning season.

There are indications that territorial defense before and during the spawning season may serve another, subsidiary function: provision of an adequate food supply for the resident fish. Observations have shown that males forage almost exclusively within their territories during the spawning season. If a cunner is not to be forced to forage away from the territory, both conspecifics and contraspecifics with similar diets must be prevented from feeding within it. The brief absences noted among some of the males may be indicative of a scarcity of prey within their territories.

With regard to conspecific competitors, transient females not receptive to courtship and male intruders are always chased. Although territorial females are present in some territories, the constant presence of a potentially receptive female may offset the disadvantages of competition for prey. Territorial females are usually found in areas with rubble substrate, and not on bare bedrock where both shelter and benthic prey would be less abundant.

Interactions with contraspecifics also suggest defense of a food supply by territorial males. Interspecific aggression has been identified as an important component of territory defense in a number of coral reef species which maintain territories outside of the reproductive season (Low, 1971; Nursall, 1974; Myrberg and Thresher, 1974). Defense of shelter, food supply, or spawn are possible functions of interspecific territoriality (Thresher, 1976 a., b.). Pomacentrus flavicauda, a herbivorous species, defends the entire home range as a territory and exhibits aggression towards 38 omnivorous or herbivorous species, but not to carnivores (Low, 1971).

It is doubtful that any of the species chased by territorial T. adspersus pose a threat to shelter availability. Capelin, flounder, and cod are not normally found in crevices in the substrate. Although P. gunnellus does seek shelter in rocky substrates, the species is considerably smaller than the cunner and there is little overlap in shelter size requirements.. Ocean pouts, Macrozoarces americanus, occupied crevices in several territories but were too large to be displaced by a cunner. In a territory where a single large crevice was available for shelter it was used by both the resident cunner and an ocean pout. However, the temporal overlap in occupancy was probably small as ocean pouts are active nocturnally.

Defense of a food resource is a more probable cause of interspecific aggression in T. adspersus. Aggression towards flounder and cottids was most frequent during and just after spawning runs of Mallotus villosus. During this period all three species were in competition for injured capelin and dead fish found on the substrate. The single observed chase of a capelin by a cunner was more likely an attempt to capture it than to exclude the fish from a territory. The rock gunnel, which feeds on shrimp, amphipods, and marine worms, may be a constant source of competition for benthic prey. Pholis gunnellus was the only contraspecific intruder consistently chased by territorial male T. adspersus.

Female territorial behaviour in T. adspersus is a rather puzzling phenomenon. The limited data suggest that, as in the case of males, the territory functions primarily as a spawning site from which potential rivals are excluded. Four of the five recorded spawns by these fish occurred within their territories. Furthermore, most territories were vacated by mid-August, after the peak of spawning activity and at a period when most females were spent. It is not known whether female territoriality is also associated with defense of a food resource. Although females' territories are far smaller than males', this does not necessarily imply that they are inadequate in terms of food availability. Females, unlike males, do not exert energy through courtship behaviour, rarely engage in 'border disputes' with conspecifics and, due to the small size of their territories, would be expected to expend less energy in their defense. However, as the timing and energy requirements of gonadal maturation are unknown, it is possible that the expected greater expenditure by females in egg development would offset the energetic advantages associated with defense of a small territory.

Territorial females do appear to graze on zooplankton more frequently than males and may compensate for a lack of benthic prey in this manner. In addition, females are more readily attracted to bait outside the territory than are males. This may indicate that territorial females are less restricted in their movements (or hungrier) than males and might be more likely to forage off the territory between spawns.

The small size of females' territories and their location on or near the borders of males' territories may be determined by male agonistic behaviour. Sale (1974) noted that where food was plentiful, maturing Pomacentrus wardi were able to establish territories on the boundaries between areas defended by older fish. The single observed attempt to establish a new territory by a male cunner occurred on a boundary between previously occupied areas. These observations suggest that some territorial species are less aggressive toward conspecifics on the periphery of the territory than to those in the central area. In combination with their colouration, which presumably will elicit courtship rather than aggression, and a failure to flee when approached by a male, which can signify receptivity to courtship, this may account for both toleration of females in a male's territory on a continual basis, and their presence in peripheral areas.

The proportion of females which exhibit territorial behaviour is unknown, although data from tagged fish indicate that up to 25% of females are territorial during the spawning season. With the present data there is no readily apparent advantage in territorial defense by female cunners. It is clear that there are both territorial and nonterritorial females, and that both behavioural 'types' spawn. All appear capable of multiple spawns per day and per season.

Although this aspect of the discussion is speculative, an advantage to female territorial behaviour can be seen if territorial males are unable to fertilize all females' spawn and if group spawners are not available to 'take up the slack.' Under such conditions competition between females for spawning partners would be expected, with restricted access to males as a possible result. Presumably, territorial females are successful in preventing some nonterritorial fish from entering a male's territory. With fewer transient females available as spawning partners, there would be an increased probability that the male could fertilize all eggs produced by the territorial females.

The Broad Cove cunner population may represent a reproductive system in transition from that in southern waters where all fish may have an opportunity to spawn, either in groups or pairs, to one in which competition is required for access to spawning partners in both sexes.

SUMMARY

1. Some male T. adspersus defend territories against both conspecific and contraspecific intruders from early June until at least late September. Most fish occupy the same territories from year to year.

2. Data indicates that the majority of territorial males are larger than 210 mm TL and at least 7 years old.

3. Nonterritorial males are vigourously excluded from territories and appear to contribute little to the reproductive output of the species.

4. Nonterritorial, sexually mature males with either juvenile or adult colouration occasionally attempt to join spawning pairs during gamete release.

5. A number of females defend small territories in the peripheral areas of some males' territories during the spawning season, and exhibit aggressive behaviour toward other females.

6. Territorial females usually spawn within their territories, with the male in whose territory they reside, although some may be promiscuous.

7. The primary function of territorial behaviour in both sexes appears to be defense of a spawning area from which potential rivals are excluded.

8. Both territorial and nonterritorial females spawn with territorial males. Nonterritorial females are thought to be promiscuous.

9. Both sexes are capable of multiple spawns.

10. Group spawning by nonterritorial fish has not been observed.

11. Spawning occurs over a 4 - 6 week period from early July to mid-August, and reaches a peak in the third week of July.

12. Courtship behaviour and agonistic interactions between adjacent territorial males gradually decrease in frequency as the spawning season progresses.

13. On a daily basis, approaches and courtship displays to female intruders by territorial males are more frequent after 1300 hrs than before, and reach a peak in frequency between 1800 and 1900 hrs. Spawns occur between 1300 and 2100 hrs.

14. Significantly more spawns and approaches to female intruders by territorial males are observed during the mid-flood to high tide phase of the tidal cycle.

15. Territorial males and females confined without food in a mesh cage on the substrate, for 5 - 7 days during the spawning season, exhibit increased frequency and duration of agonistic interactions with adjacent territorial fish upon return to their territories. Nonterritorial fish do not exhibit aggression toward conspecifics after release.

LITERATURE CITED

Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. U.S. Fish and Wildl. Serv. Bull., 53 (74).

Costello, D. P., Davidson, M. E., Eggars, A., Fox, M. H., and C. Henley. 1957. Methods for obtaining and handling marine eggs and embryos. Mar. Biol. Lab. Woods Hole, Mass.

Dew, C. A. 1976. A contribution to the life history of the cunner, *Tautogolabrus adspersus*, in Fishers Island Sound, Connecticut. Ches. Sci. 17(2): 101 - 113.

Green, J. M. and M. Farwell. 1971. Winter habits of the cunner, *Tautogolabrus adspersus* (Walbaum 1792), in Newfoundland. Can. J. Zool. 53: 1497 - 1499.

Green, J. M. 1975. Restricted movements and homing of the cunner, *Tautogolabrus adspersus* (Walbaum) (Pisces: Labridae). Can. J. Zool. 53: 1427 - 1431.

Haugaard, N. and L. Irving. 1943. The influence of temperature upon the oxygen consumption of the cunner (*Tautogolabrus adspersus* Walbaum) in summer and in winter. J. Cell. Comp. Physiol. 21(1): 19 - 26.

Hobson, E. S. 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965: 291 - 302.

Hobson, E. S. 1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull. 70: 715 - 740.

Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fish. 3: 65 - 84.

Johansen, F. 1925. Natural history of the cunner (*Tautogolabrus adspersus* Walbaum). Contr. Can. Biol. 2(17): 423 - 468.

Kuntz, A. and L. Radcliffe. 1918. Notes on the embryology and larval development of twelve teleostean fishes. Fish. Bull. U.S. 35: 87 - 134.

Liem, A. H., and W. B. Scott. 1966. Fishes of the Atlantic coast of Canada. Fish. Res. Board. Can., Bull. 155, 485 p.

Low, R. M. 1971. Interspecific territoriality in a pomacentrid reef fish, *Pomacentrus flavicauda* Whitley. Ecology 52: 648 - 654.

McErlean, A. J. 1963. Aquarium behaviour of juvenile labrid fishes. Copeia 1963(1): 186.

Meyer, K. A. 1977. Reproductive behaviour and patterns of sexuality in the Japanese labrid fish *Thalassoma cupido*. Jap. J. Icthyol. 24: 101 - 112.

Moyer, J. T. and J. W. Shepard. 1975. Notes on the spawning behaviour of the wrasse, *Crenilabrus terminickii*. Jap. J. Icthyol. 22: 40 - 42.

Myrberg, A. A. Jr. and R. E. Thresher. 1974. Interspecific aggression and its relevance to the concept of territoriality in reef fishes. Amer. Zool. 14: 81 - 96.

Naidu, K. S. 1966. The age, growth, distribution, and development of the commercially unexploited cunner, *Tautogolabrus adspersus* (Walbaum 1792) in Newfoundland coastal waters. B. Sc. Thesis (Honors), Memorial University of Nfld., St. John's. 151 p.

Nakazono, A. and H. Tsukahara. 1974. Underwater observation on the spawning behaviour of the wrasse, *Duymaeria flagellifera* (Cuvier et Valenciennes). Report Fish Res. Lab., Kyusha Univ. 2: 1 - 11.

Noble, G. K. 1938. Sexual selection among fishes. Biol. Rev. 13: 133 - 158.

Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K., and D. H. Brent. 1975. Statistical package for the social sciences. 2nd ed. McGraw - Hill Book Co. N.Y. p.320 - 360.

Nursall, J. R. 1974. Some territorial behavioural attributes of the surgeonfish *Acanthurus lineatus* at Heron Island, Queensland. Copeia 1974(4): 950 - 959.

Olla, B. L. Bejda, A. J. and A. D. Martin. 1975. Activity, movements, and feeding behaviour of the cunner, *Tautogolabrus adspersus*, and comparison of food habits with young tautog, *Tautoga onitis*, off Long Island, N.Y. Fish. Bull, U.S. 73(4): 895 - 900.

Olla, B. L. and C. Samet. 1977. Courtship and spawning behaviour of the tautog, *Tautoga onitis* (Pisces: Labridae), under laboratory conditions. Fish. Bull, U.S. 75(3): 585 - 599.

Olla, B. L., Samet, C., Bejda, A. J., and A. L. Studholme. 1977. Social behaviour as related to environmental factors in the tautog, *Tautoga onitis*. Behaviour of Marine Organisms. Proc. Ann. Northeast. Reg. Meet. Anim. Behav. Soc. 1977: Plenary papers. MSRL Tech. Rep. 20: 47 - 99.

Payne, J. F. 1976. Field evaluation of benzopyrene hydroxylase induction as a monitor for Marine petroleum polution. Science 191: 945 - 946.

Potts, G. W. 1974. The colouration and its behavioural significance in the corkwing wrasse, *Crenilabrus melops*. J. Sar. Biol. Assoc. U.K. 54: 925 - 938.

Randall, J. E. and H. A. Randall. 1963. The spawning and early development of the Atlantic parrot fish, *Sparisoma rubripinne* with notes on other scarid and labrid fishes. Zoologica (N.Y.) 48: 47 - 60.

Reid, M.E. 1929. The distribution and development of the cunner (*Tautogolabrus adspersus* Walbaum) along the eastern coast of Canada. Contr. Can. Biol. and Fish. 4: 433-441.

Reinboth, R. 1973. Dualistic reproductive behaviour in the protogynous wrasse *Thalassoma bifasciatum* and some observations on its day-night changeover. Heligolander wiss. Meersunters 24: 174 - 191.

Robertson, D.R. and J.H. Choat. 1974. Protogynous hemaphroditism and social systems in labrid fish. Proc. 2nd. Int. Symp. Coral Reefs 1: 217 - 225.

Robertson, D.R. and S.G. Hoffman. 1977. The roles of female mate choice and predation in the mating systems of some tropical labroid fishes. Z. Tierpsychol. 45: 298 - 320.

Roede, M.J. 1972. Color as related to size, sex, and behavior in seven Caribbean labrid fish species (genera *Thalassoma*, *Halichoeres*, and *Hemipternotus*). Stud. Fauna Curacao Other Caribb. Isl. 42 (138), 264 pp.

Sale, P.F. 1974. Mechanisms of co-existence in a guild of territorial fishes at Heron Island. Proc. 2nd. Int. Symp. Coral Reefs 1: 193 - 215.

Selander, R.K. 1965. On mating systems and sexual selection. Amer. Natur. 99 (906): 129 - 141.

Sokal, R.R. and F.J. Rohlf. 1969. Biometry. The principles and practice of statistics in biological research. W.H. Freeman and Co., San Francisco. p. 320 - 328, 575 - 585.

Thresher, R.E. 1976 a. Field analysis of the territoriality of the threespot damselfish, *Eupomacentrus planifrons* (Pomacentridae). Copeia 1976 (2): 266 - 276.

Thresher, R.E. 1976 b. Field experiments on species recognition by the threespot damselfish, *Eupomacentrus planifrons*, (Pisces: Pomacentridae). Anim. Behav. 24: 562 - 569.

Warner, R.R., Robertson, D.R. and E.G. Leigh Jr. 1977. Sex change and sexual selection. Sci. 190: 633 - 638.

Wicklund, R.I. 1970. Observations on the spawning of the cunner in the waters of northern New Jersey. Chesapeake Sci. 11: 137.

Youngbluth, M.J. 1968. Aspects of the ecology and ethology of the cleaning fish, *Labroides phthirophagus* Randall. Z. Tierpsychol. 25: 915 - 932.

ADDENDUM

Ambrose, J. 1870. On fishes of St. Margaret's Bay. Proc. Trans. Nova Scotia Inst. Natur. Sci., 2(2): 87 - 94.

Shumway, S. and R. Stickney. 1975. Notes on the biology and food habits of the cunner. N.Y. Fish and Game Jour. Vol. 22(1): 71 - 79.

APPENDIX

Raw Data:

Data collected during 442 field observations of territorial male *Tautogolabrus adspersus* are tabulated below. In each horizontal row are the parameter values obtained from a single 15 min observation. Parameters are:

WEEK - from start of observations (6 July, 1977)
DAY - from start of observations
TIME - hour of observation
TIDE - tidal phase
TEMP - temperature in C°
TAG - tag number
APPR - number of approaches observed
CHASE - number of chases observed
LATER - number of lateral displays observed
FRONT - number of frontal displays observed
CA - number of courtship approaches observed
SPAWN - number of spawns observed

WEEK	DAY	TIME	TIDE	TEMP	TAG	APPR	CHASE	LATER	FRONT	CA	SPAWN
1	1	1400	1		07	4	1	1	2		0
1	1	1400	2		11	2	1	1	0		0
1	1	1500	2		08	2	2	1	0		0
1	1	1500	2		19	8	0	1	0		0
1	2	1300	1	11.0	17	9	1	3	0		0
1	2	1300	1	11.0	11	3	1	0	0		0
1	2	1300	1	11.0	26	3	2	1	0		0
1	2	1300	1	11.0	25	5	3	1	0		0
1	2	1400	1	11.0	21	5	3	0	2		0
1	2	1400	1	11.0	23	8	5	0	0		0
1	2	1400	1	11.0	25	6	2	3	2		0
1	2	1400	1	11.0	17	5	1	0	0		0
1	2	1500	1	11.0	22	3	1	1	1		0
1	2	1500	2	11.0	23	5	1	0	0		0
1	2	1500	2	11.0	07	5	1	0	0		0
1	2	1500	2	11.0	22	6	1	0	0		0
1	4	1600	1		26	10	1	2	0		0
1	4	1600	1		21	4	1	0	0		0
1	4	1600	1		08	18	1	1	0		0
1	4	1600	1		19	13	8	2	1		0
1	4	1600	1		22	4	0	0	0		0
1	4	1600	1		26	16	3	1	0		0
1	4	1600	1		17	18	4	1	1		0
1	4	1600	1		23	8	0	3	0		0
1	4	1700	1		21	15	2	1	3		0
1	4	1700	1		11	9	2	0	0		0
1	4	1700	2		07	35	1	1	0		0
1	4	1700	2		19	12	4	0	0		0
1	4	1700	2		08	38	0	2	2		0
1	4	1700	2		24	12	4	1	0		0
1	6	1200	3	12.0	23	3	0	1	0		
1	6	1200	3	12.0	17	4	0	2	0		
1	6	1200	3	12.0	24	9	0	0	0		
1	6	1200	3	12.0	26	4	1	3	1		
1	6	1200	3	12.0	08	7	0	1	1		
1	6	1200	3	12.0	19	6	3	1	0		
1	6	1300	3	12.0	11	1	0	0	0		0
1	6	1300	3	12.0	21	0	0	0	0		0
1	6	1300	4	12.0	22	7	1	0	0		0
1	6	1300	4	12.0	07	7	0	0	0		0
1	6	1900	4	12.0	26	17	0	1	0		0
1	6	1900	4	12.0	25	11	6	0	0		0
1	6	1900	1	12.0	08	16	1	2	0		0
1	6	1900	1	12.0	11	13	2	3	0		0
1	6	2000	1	12.0	21	1	1	0	0		0
1	6	2000	1	12.0	23	3	1	1	0		0
[illegible]	6	2000	1	12.0	22	9	0	1	1		0
1	6	2000	1	12.0	07	8	5	2	0		0
1	6	2000	1	12.0	19	13	3	0	0		0
1	6	2000	1	12.0	17	16	10	1	0		0
1	7	1800	1	12.0	23	18	2	0	0		0
1	7	1800	1	12.0	21	9	0	0	0		0

1	7	1900	1	12.0	26	15	1	0	0	0
1	7	1900	1	12.0	08	14	4	0	0	0
1	7	1900	1	12.0	11	19	4	1	0	1
1	7	1900	1	12.0	08	16	7	1	0	0
1	7	1900	1	12.0	17	14	5	0	0	0
1	7	1900	1	12.0	22	14	4	2	0	0
1	7	1900	1	12.0	19	14	3	0	0	0
1	7	1900	1	12.0	25	6	2	1	0	0
2	8	0700	1	12.5	08	8	0	4	0	
2	8	0700	1	12.5	17	8	1	0	0	
2	8	0800	1	12.4	26	6	1	0	0	
2	8	0800	1	12.5	25	3	1	0	0	
2	8	0800	1	12.5	07	10	3	0	0	
2	8	0800	1	12.5	22	10	2	0	0	
2	8	0800	1	12.5	19	13	8	1	1	
2	8	0800	1	12.5	23	4	0	1	1	
2	8	0800	1	12.5	21	2	0	0	0	
2	8	0800	1	12.5	11	3	0	0	0	
2	8	1600	4	13.0	07	32	1	1	1	1
2	8	1600	4	13.0	23	26	4	0	0	0
2	8	1600	4	13.0	22	18	3	3	1	0
2	8	1600	4	13.0	08	50	8	1	1	1
2	8	1700	4	13.0	17	32	4	0	0	0
2	8	1700	4	13.0	11	24	2	3	2	1
2	8	1700	4	13.0	25	33	9	0	0	0
2	8	1700	4	13.0	19	26	0	0	0	0
2	8	1700	4	13.0	21	27	0	0	1	1
2	8	1700	4	13.0	27	50	10	0	0	2
2	9	0900	1	12.0	08	1	0	0	0	
2	9	0900	1	12.0	25	13	1	1	0	
2	9	0900	2	12.0	23	14	4	2	1	
2	9	0900	2	12.0	11	5	1	3	1	
2	9	1000	2	12.0	26	21	3	1	0	0
2	9	1000	2	12.0	19	12	3	1	0	0
2	9	1000	2	12.0	17	13	5	1	0	0
2	9	1000	2	12.0	21	7	2	0	0	0
2	9	1000	2	12.0	07	14	5	0	0	0
2	9	1000	2	12.0	22	9	2	0	1	0
2	9	1700	4	13.0	26	21	5	2	2	0
2	9	1700	4	13.0	23	21	2	0	0	0
2	9	1700	4	13.0	22	17	3	1	1	0
2	9	1700	4	13.0	25	26	3	1	1	0
2	9	1700	4	13.0	21	34	0	1	2	0
2	9	1700	4	13.0	07	32	3	1	1	1
2	9	1700	4	13.0	08	16	0	0	0	0
2	9	1700	4	13.0	19	18	1	1	0	0
2	9	1800	4	13.0	17	22	5	0	0	1
2	9	1800	4	13.0	11	26	3	1	1	1
2	10	1100	2	12.5	21	2	0	0	0	
2	10	1100	2	12.5	07	14	1	1	0	
2	10	1100	2	12.5	26	10	0	15	2	
2	10	1100	2	12.5	23	7	0	1	0	
2	10	1100	2	12.5	19	8	4	1	0	
2	10	1100	2	12.5	11	3	0	0	0	

2	10	1200	2	12.5	25	19	3	3	0		
2	10	1200	2	12.5	17	12	3	0	0		
2	10	1200	2	12.5	08	4	1	1	0		
2	10	1200	2	12.5	22	19	5	0	0		
2	10	1800	4	14.0	26	25	3	1	0		1
2	10	1800	4	14.0	23	54	8	1	0		1
2	10	1900	4	14.0	25	24	8	3	0		0
2	10	1900	4	14.0	07	31	4	1	1		2
2	10	1900	4	14.0	17	19	3	0	0		0
2	10	1900	4	14.0	11	35	7	0	0		1
2	10	1900	4	14.0	21	25	6	0	1		0
2	10	1900	4	14.0	22	16	5	2	1		0
2	10	1900	1	14.0	19	7	2	0	0		0
2	10	1900	1	14.0	08	17	2	1	1		0
2	11	1800	4	14.0	19	10	1	0	0		0
2	11	1800	4	14.0	08	17	4	0	0		0
2	11	1800	4	14.0	25	13	2	4	2		1
2	11	1800	4	14.0	07	17	3	1	1		1
2	11	1900	4	14.0	11	11	5	3	0		0
2	11	1900	4	14.0	26	13	1	1	1		0
2	11	1900	4	14.0	22	22	2	0	0		0
2	11	1900	4	14.0	21	5	2	0	0		0
2	11	1900	4	14.0	23	24	1	2	1		0
2	11	1900	4	14.0	17	16	6	0	0		0
2	12	1500	3	14.0	07	55	3	0	1		0
2	12	1500	3	14.0	23	20	3	1	0		0
2	12	1500	3	14.0	22	26	3	0	0		0
2	12	1600	3	14.0	25	32	0	6	0		0
2	12	1600	3	14.0	19	33	0	0	0		0
2	12	1900	4	14.0	11	8	2	2	1		0
2	12	1900	4	14.0	08	12	2	0	0		0
2	12	2000	4	14.0	21	7	2	0	1		0
2	13	1000	1	14.0	26	13	1	1	0		0
2	13	1000	1	14.0	07	6	4	0	0		0
2	13	1100	1	14.0	21	6	0	0	0		
2	13	1100	1	14.0	23	7	1	3	2		
2	13	1100	1	14.0	25	14	2	0	0		
2	14	0600	4	12.5	17	19	5	3	0	3	
2	14	0600	3	12.5	11	5	2	1	0	0	
2	14	0600	3	12.5	08	7	1	0	0	0	
2	14	0700	4	12.5	22	12	2	2	1	0	
2	14	0700	4	12.5	19	14	3	4	0	0	
2	14	0900	4	14.0	17	15	5	4	1	1	
2	14	0900	4	14.0	22	10	1	0	0	0	
2	14	0900	1	14.0	25	12	3	1	1	0	
2	14	1000	1	14.0	21	4	1	5	1	1	
2	14	1000	1	14.0	07	9	2	1	0	1	
2	14	1200	1	15.0	11	1	1	0	0	0	
2	14	1200	1	15.0	26	21	3	4	0	4	
2	14	1200	1	15.0	25	17	4	2	0	3	
2	14	1200	2	15.0	19	18	0	0	0	8	
2	14	1300	2	15.0	08	17	2	1	0	8	0
3	16	0700	3	13.0	19	11	4	0	0	0	
3	16	0700	3	13.0	11	14	10	0	0	0	

3	16	0700	3	13.0	17	13	6	0	0	1	
3	16	0700	4	13.0	21	10	0	0	0	1	
3	16	0800	4	13.0	26	13	3	7	0	0	
3	16	0800	4	13.0	08	12	3	0	0	1	
3	17	1600	2		25	22	3	2	0	5	0
3	17	1600	2		23	20	2	0	0	5	0
3	17	1600	2		07	49	1	0	0	32	0
3	17	1700	3		22	29	1	1	2	7	0
3	19	1300	1	10.0	23	19	3	1	0	3	0
3	19	1300	1	10.0	11	4	1	1	0	0	0
3	19	1400	1	10.0	07	13	1	0	0	3	1
3	19	1400	1	10.0	08	1	0	0	0	0	0
3	19	1400	1	10.0	19	2	0	0	0	0	0
3	19	1900	2	9.0	26	0	0	0	0	0	0
3	19	1000	2	9.0	11	2	0	0	0	0	0
3	19	1000	2	9.0	22	10	1	0	0	0	0
3	19	2000	2	9.0	25	9	3	0	0	0	0
3	19	2000	2	9.0	17	1	0	3	0	0	0
3	20	0600	2	10.0	21	3	0	0	0	0	
3	20	0700	2	10.0	26	26	2	1	1	1	
3	20	0700	2	10.0	19	3	1	0	0	0	
3	20	0700	2	10.0	08	0	0	0	0	0	
3	20	0700	2	10.0	21	5	0	0	0	0	
3	20	1500	1	10.5	25	6	1	0	0	0	0
3	20	1500	1	10.5	23	11	1	2	1	2	0
3	20	1500	1	10.5	07	4	0	0	0	0	0
3	20	1600	1	10.5	17	0	0	0	0	0	0
3	20	1600	1	10.5	22	12	3	3	0	3	1
3	20	1900	2	10.5	19	1	0	1	0	0	0
3	20	2000	2	10.5	11	3	2	0	0	0	0
3	20	2000	2	10.5	26	12	5	1	1	3	0
3	20	2000	2	10.5	08	2	0	2	0	0	0
3	21	1200	3	9.5	22	11	1	0	0	0	
3	21	1200	3	9.5	17	6	1	0	0		
3	21	1200	4	9.5	21	0	0	0	0	0	
3	21	1200	4	9.5	23	8	5	0	0		
3	21	1300	4	9.5	07	13	0	3	2	0	0
3	21	1300	4	9.5	19	1	0	0	0		0
3	21	1300	4		25	2	0	0	0	0	0
3	21	1300	4		11	6	0	2	0		0
4	23	1300	3		07	16	5	0	0	2	0
4	23	1300	3		25	0	0	0	0	0	0
4	23	1400	3		23	5	2	0	0	1	0
4	23	1400	3		21	6	0	0	0	0	0
4	23	1400	3		17	13	0	0	0	8	1
4	23	1800	1	14.0	08	22	5	1	0	3	0
4	24	1100	2	14.0	26	5	2	0	0	1	
4	24	1100	2	14.0	22	10	4	0	0	0	
4	24	1100	2	14.0	11	9	2	0	0	1	
4	24	1100	2	14.0	21	9	0	3	0	0	
4	24	1200	2	14.0	23	3	1	0	0	0	
4	24	1200	2	14.0	19	3	2	0	0	0	
4	24	1200	2	14.0	26	9	3	0	0	0	
4	24	1200	3	14.0	08	2	1	0	0	0	

4	24	1200	3	14.0	22	10	2	0	0	1	
4	24	1200	2	14.0	25	2	0	0	0	0	
4	24	1600	4	14.0	07	18	2	0	0	7	1
4	24	1600	4	14.0	17	18	4	0	0	2	0
4	24	1700	4	14.0	17	21	6	0	0	3	0
4	24	1700	4	14.0	23	39	4	2	1	19	1
4	24	1700	4	14.0	11	7	0	0	0	10	1
4	24	1700	4	14.0	22	10	0	0	0	1	0
4	24	1700	4	14.0	25	17	1	1	0	6	0
4	24	1700	4	14.0	19	7	1	0	0	0	0
4	27	1200	2		21	8	1	3	0	0	
4	27	1200	2		08	0	0	0	0	0	
4	27	1300	2		08	2	0	0	0	0	0
4	27	1300	2		26	5	2	0	0	0	0
4	27	1300	2		11	4	0	0	0	0	0
4	27	1300	2		07	8	2	1	0	0	0
4	27	1300	2		25	7	1	0	0	0	0
4	27	1300	2		21	1	0	1	0	0	0
4	27	1300	2		26	5	2	0	0	0	0
4	27	1300	2		19	5	0	0	0	0	0
4	27	1400	2		17	4	1	2	0	0	0
4	27	1600	3		23	9	4	2	0	2	0
4	27	1600	3		07	7	0	1	0	1	0
4	27	1600	3		07	8	3	4	0	0	0
4	27	1600	3		11	8	2	0	0	4	0
4	27	1600	3		22	1	5	1	1	1	0
4	27	1600	3		25	3	1	0	0	0	0
4	27	1600	3		19	5	3	0	0	0	0
4	27	1600	3		17	11	0	2	0	0	0
4	27	1700	3		21	9	1	4	0	0	0
4	27	1700	3		26	7	3	0	0	3	0
4	27	1700	3		08	2	0	0	0	0	0
4	27	1800	4		23	14	6	0	1	0	0
4	27	1800	4		22	3	0	0	0	0	0
4	27	1900	4		26	6	1	0	0	0	0
4	27	1900	4		17	9	3	0	0	0	0
4	28	0700	4		11	4	1	0	0	0	0
4	28	0800	4		19	5	1	0	0	0	0
4	28	0800	4		23	13	5	1	0	0	
4	28	0800	4		25	3	0	0	0	0	
4	28	0900	1		21	9	1	2	0	0	
4	28	0900	1		22	2	1	0	0	0	
4	28	1000	1		07	4	2	2	0	0	
4	28	1000	1		08	2	1	0	0	0	
5	29	1100	1		08	3	0	0	0	0	
5	29	1100	1		19	7	2	0	0	0	
5	29	1100	1		22	3	0	0	0	0	
5	29	1100	1		26	10	4	1	0	0	
5	29	1100	1		25	11	5	1	0	0	
5	29	1100	1		21	10	0	2	0	0	
5	29	1200	1		23	9	3	0	0	0	
5	29	1200	1		17	6	1	0	0	0	
5	29	1200	1		11	5	1	1	0	1	
5	29	1200	1		07	6	3	0	0	0	

5	29	1400	2	13.0	25	20	1	0	0	5	0
5	29	1400	2	13.0	08	5	2	0	0	0	0
5	29	1400	2	13.0	11	20	4	3	0	30	0
5	29	1400	2	13.0	07	22	6	2	1	1	0
4	29	1400	2	13.0	22	6	3	0	0	1	0
5	29	1400	2	13.0	21	10	0	3	0	0	0
5	29	1400	2	13.0	19	15	2	0	0	4	0
5	29	1400	2	13.0	23	15	2	0	0	0	0
5	29	1500	2	13.0	26	22	4	0	0	3	0
5	29	1500	2	13.0	17	16	0	0	0	8	0
5	29	2000	4	13.0	11	7	2	1	0	1	0
5	29	2000	4	13.0	21	8	3	1	0	0	0
5	29	2000	4	13.0	17	5	2	0	0	0	0
5	29	2000	4	13.0	07	8	5	0	0	0	0
5	30	1600	2	15.0	08	32	11	0	0	5	0
5	30	1600	2	15.0	19	9	3	0	0	1	0
5	30	1600	2	15.0	22	24	5	1	0	2	0
5	30	1600	2	15.0	23	65	41	0	0	0	0
5	30	1700	2	15.0	26	15	0	0	0	3	1
5	30	1700	2	15.0	25	22	10	2	0	0	0
5	30	1700	3	15.0	25	27	8	2	0	1	1
5	30	1700	3	15.0	08	10	7	0	0	0	0
5	30	1700	3	15.0	23	25	4	0	0	5	0
5	30	1700	3	15.0	22	22	10	0	0	1	0
5	30	1800	3	15.0	11	32	5	1	0	10	1
5	30	1800	3	15.0	26	17	6	0	0	1	0
5	30	1900	3	15.0	26	3	2	0	0	0	0
5	30	1900	3	15.0	21	8	3	0	0	0	0
5	30	2000	4	15.0	08	4	3	0	0	0	0
5	30	2000	4	15.0	07	20	15	0	0	0	0
5	30	2000	4	14.0	07	19	14	1	0	0	0
5	30	2000	4	15.0	17	12	7	1	0	0	0
5	31	0900	4	13.5	19	10	2	0	0	0	
5	31	0900	4	13.5	22	3	0	0	0	0	
5	31	1000	4	13.5	11	9	3	0	0	1	
5	31	1000	4	13.5	19	1	0	0	0	0	
5	31	1000	4	13.5	21	10	2	2	0	0	
5	31	1000	4	13.5	17	4	0	1	1	0	
5	31	1000	4	13.5	23	17	5	0	0	0	
5	31	1000	4	13.5	25	12	5	0	0	0	
5	31	1200	1	14.5	23	20	9	1	0	0	
5	31	1200	1	14.5	26	9	3	1	0	2	
5	31	1200	1	14.5	21	2	0	0	0	0	
5	31	1200	1	14.5	19	7	2	0	0	0	
5	31	1200	1	14.5	17	11	1	0	0	3	
5	31	1200	1	14.5	07	15	7	0	0	0	
5	31	1300	1	14.5	22	17	7	2	0	0	0
5	31	1300	1	14.5	11	19	8	0	0	0	0
5	31	1300	1	14.5	25	5	1	0	0	0	0
5	31	1300	1	14.5	08	9	4	0	0	1	0
5	31	1400	1	14.5	25	4	1	0	0	0	0
5	31	1400	1	14.5	23	37	20	0	0	0	0
5	31	1400	1	14.5	26	16	3	3	0	1	0
5	31	1400	1	14.5	21	16	4	2	0	0	0

5	31	1400	2	14.5	19	19	1	0	0	8	0
5	31	1400	2	14.5	17	35	4	0	0	10	0
5	31	1500	2	14.5	07	21	2	0	10	1	
5	31	1500	2	14.5	22	28	14	0	0	1	0
5	31	1800	3	15.0	11	17	10	2	0	4	0
5	31	1800	3	15.0	08	5	0	0	0	1	0
5	31	1900	3	15.0	08	3	1	0	0	0	0
5	31	1900	3	15.0	22	35	0	0	0	13	0
5	31	1900	3	15.0	23	20	8	0	0	1	0
5	31	1900	3	15.0	17	11	3	1	0	0	0
5	31	1900	3	15.0	11	22	11	0	0	3	0
5	31	1900	3	15.0	21	14	5	3	0	0	0
5	31	1900	3	15.0	07	24	18	0	0	0	0
5	31	1900	3	15.0	26	11	5	1	0	0	0
5	32	0700	3	13.0	22	13	3	0	0	0	
5	32	0700	3	13.0	17	2	1	0	0	0	
5	32	0700	3	13.0	23	18	2	0	0	0	
5	32	0700	3	13.0	25	12	6	0	0	0	
5	32	0700	3	13.0	26	6	1	1	3	0	
5	32	0700	3	13:0	19	7	2	0	0	0	
5	32	0700	3	13.0	17	16	2	5	0	0	
5	32	0700	3	13.0	08	2	2	0	0	0	
5	32	0800	3	13.0	19	10	1	3	0	0	
5	32	0800	3	13.0	07	6	4	1	0	0	
5	32	1000	4	13.0	25	4	2	0	0	0	
5	32	1000	4	13.0	08	4	2	0	0	0	
5	32	1000	4	13:0	22	11	3	1	0	0	
5	32	1000	4	13.0	17	7	2	1	0	0	
5	32	1100	4	13.0	23	19	11	0	0	0	
5	32	1100	4	13.0	07	10	6	1	0	0	
5	32	1100	4	13.0	11	10	5	0	0	0	
5	32	1100	4	13.0	19	14	4	1	0	0	
5	32	1100	5	13.0	26	10	3	0	0	0	
5	32	1100	4	13.0	21	4	0	1	0	0	
5	32	1100	4	13.0	25	10	6	0	0	0	
5	32	1100	4	13.0	19	15	6	2	0	0	
5	32	1600	2	13.0	08	10	5	0	0	0	0
5	32	1600	2	13.0	22	8	2	1	0	0	0
5	32	1600	2	13.0	17	16	8	1	0	0	0
5	32	1700	2	13.0	23	38	4	1	0	0	0
5	32	1700	2	13.0	07	26	3	1	1	3	0
5	32	1700	2	13.0	11	36	5	0	0	19	0
5	32	1700	2	13.0	19	12	5	0	0	1	0
5	32	1700	2	13.0	26	12	0	0	0	1	0
5	32	1700	2	13.0	21	10	2	0	0	2	0
5	33	1200	4	15.0	17	6	1	0	0	0	
5	33	1200	4	15.0	08	5	2	0	0	0	
5	33	1200	4	15.0	23	7	3	0	0	0	
5	33	1300	1	15.0	26	10	8	0	0	0	0
5	33	1300	1	15.0	07	14	5	0	0	1	0
5	33	0800	3	12.5	19	10	5	0	0	0	
5	33	0800	3	12.5	25	14	7	0	0	0	
5	33	0900	3	12.5	22	6	2	2	0	0	
5	33	0900	3	12.5	21	5	0	1	0	0	

5	33	0900	3	12.5	11	9	3	2	0	0	
5	35	1000	3	15.0	21	14	3	0	0	0	
5	35	1000	3	15.0	25	7	2	0	0	0	
5	35	1100	3	15.0	07	15	10	0	0	3	
5	35	1100	3	15.0	22	13	5	0	0	0	
5	35	1100	3	15.0	17	14	7	1	0	0	
5	35	1100	3	15.0	19	4	1	0	0	0	
5	35	1100	3	15.0	26	40	5	2	0	0	
5	35	1100	3	15.0	23	5	3	0	0	0	
5	35	1100	3	15.0	08	11	2	0	0	2	
5	35	1100	3	15.0	11	17	4	0	0	0	
5	35	1300	4	16.5	21	8	4	1	0	0	1
5	35	1300	4	16.5	19	3	1	0	0	0	0
5	35	1300	4	16.5	17	30	4	0	0	3	0
5	35	1300	4	16.5	08	10	1	0	0	4	0
5	35	1400	4	16.5	11	23	7	0	0	3	0
5	35	1400	4	16.5	22	24	7	0	0	1	0
5	35	1400	4	16.5	25	34	10	0	0	0	0
5	35	1400	4	16.5	23	20	12	0	0	2	0
5	35	1400	4	16.5	07	36	8	0	0	11	0
5	35	1400	4	16.5	26	26	4	0	0	8	1
6	38	1200	3	11.0	17	9	2	0	0	0	
6	38	1200	3	11.0	23	7	3	0	0	0	
6	38	1300	3	11.0	26	3	1	1	0	0	0
6	38	1300	3	11.0	21	11	7	3	0	0	0
6	38	1300	3	11.0	11	6	2	0	0	0	0
6	35	1300	3	11.0	19	12	1	2	0	0	0
6	58	1300	3	11.0	08	3	1	1	0	0	0
6	58	1300	3	11.0	22	4	1	0	0	0	0
6	38	1400	3	11.0	07	6	5	0	0	0	0
6	38	1500	5	12.0	07	11	4	0	0	2	0
6	38	1500	3	12.0	25	4	2	0	0	0	0
6	38	1500	4	12.0	17	10	4	1	0	0	0
6	38	1500	4	12.0	23	7	3	0	0	0	0
6	38	1500	4	12.0	21	4	2	1	0	0	0
6	38	1500	4	12.0	22	4	1	0	0	0	0
6	38	1600	4	12.0	26	8	7	5	0	0	0
6	38	1600	4	12.0	11	8	2	0	0	0	0
6	38	1600	4	12.0	08	0	0	0	0	0	0
6	38	1600	4	12.0	19	4	1	0	0	0	0
6	42	1600	3	14.5	08	10	3	0	0	0	0
6	42	1600	3	14.5	11	17	4	1	0	0	0
6	42	1600	3	14.5	25	2	1	0	0	0	0
6	42	1600	3	14.5	23	24	2	0	0	0	0
6	42	1600	3	14.5	26	3	1	0	0	0	0
6	42	1700	3	14.5	17	12	1	0	0	0	0
6	42	1700	3	14.5	21	2	0	0	0	0	0
6	42	1700	3	14.5	19	10	3	0	0	0	0
7	45	1200	1	13.5	23	9	5	0	0	0	
7	45	1200	1	13.5	08	2	0	0	0	0	
7	45	1200	1	13.5	22	6	4	0	0	0	
7	45	1200	1	13.5	19	4	2	0	0	0	
7	45	1200	1	13.5	11	10	5	0	0	0	
71	45	1200	1	13.5	19	18	6	1	0	0	

7	45	1200	1	13.5	21	5	1	0	0	0	
7	45	1200	1	13.5	25	11.	3	0	0	0	
7	45	1300	1	13.5	26	11	7	1	0	0	0
7	45	1300	1	13.5	07	10	6	0	0	0	0
7	49	1100	4		23	14	5	0	0	0	
7	49	1100	4		08	3	3	0	0	0	
7	49	1100	4		26	15	0	1	0	0	
7	49	1100	4		17	16	12	0	0	0	
7	49	1100	4		07	18	5	1	0	0	
7	49	1100	4		21,	6	1	1	0	0	
7	49	1200	4		19	6	2	0	0	0	
7	49	1200	4		11	7	3	0	0	0	