



National Library
of Canada

Bibliothèque nationale
du Canada

Acquisitions and
Bibliographic Services Branch

Direction des acquisitions et
des services bibliographiques

395 Wellington Street
Ottawa, Ontario
K1A 0N4

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

NOTICE

The quality of this microform 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 an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme 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 qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

**SETTLEMENT AND POST-SETTLEMENT PROCESSES IN THE
POPULATION REGULATION OF A TEMPERATE REEF FISH:
THE ROLE OF ENERGY**

Mark Tupper

Submitted in partial fulfilment of the requirements

for the degree of Doctor of Philosophy

at

Dalhousie University

Halifax, Nova Scotia

June, 1994

© Copyright by Mark Tupper, 1994



National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

THE AUTHOR HAS GRANTED AN
IRREVOCABLE NON-EXCLUSIVE
LICENCE ALLOWING THE NATIONAL
LIBRARY OF CANADA TO
REPRODUCE, LOAN, DISTRIBUTE OR
SELL COPIES OF HIS/HER THESIS BY
ANY MEANS AND IN ANY FORM OR
FORMAT, MAKING THIS THESIS
AVAILABLE TO INTERESTED
PERSONS.

L'AUTEUR A ACCORDE UNE LICENCE
IRREVOCABLE ET NON EXCLUSIVE
PERMETTANT A LA BIBLIOTHEQUE
NATIONALE DU CANADA DE
REPRODUIRE, PRETER, DISTRIBUER
OU VENDRE DES COPIES DE SA
THESE DE QUELQUE MANIERE ET
SOUS QUELQUE FORME QUE CE SOIT
POUR METTRE DES EXEMPLAIRES DE
CETTE THESE A LA DISPOSITION DES
PERSONNE INTERESSEES.

THE AUTHOR RETAINS OWNERSHIP
OF THE COPYRIGHT IN HIS/HER
THESIS. NEITHER THE THESIS NOR
SUBSTANTIAL EXTRACTS FROM IT
MAY BE PRINTED OR OTHERWISE
REPRODUCED WITHOUT HIS/HER
PERMISSION.

L'AUTEUR CONSERVE LA PROPRIETE
DU DROIT D'AUTEUR QUI PROTEGE
SA THESE. NI LA THESE NI DES
EXTRAITS SUBSTANTIELS DE CELLE-
CI NE DOIVENT ETRE IMPRIMES OU
AUTREMENT REPRODUITS SANS SON
AUTORISATION.

ISBN 0-612-05173-0

Canada

Name Mark Tupper

Dissertation Abstracts International is arranged by broad, general subject categories. Please select the one subject which most nearly describes the content of your dissertation. Enter the corresponding four-digit code in the spaces provided.

Ecology

SUBJECT TERM

0329 U·M·I
SUBJECT CODE

Subject Categories

THE HUMANITIES AND SOCIAL SCIENCES

COMMUNICATIONS AND THE ARTS

Architecture 0729
Art History 0377
Cinema 0900
Dance 0378
Fine Arts 0357
Information Science 0723
Journalism 0391
Library Science 0399
Mass Communications 0708
Music 0413
Speech Communication 0459
Theater 0465

EDUCATION

General 0515
Administration 0514
Adult and Continuing 0516
Agricultural 0517
Art 0273
Bilingual and Multicultural 0282
Business 0688
Community College 0275
Curriculum and Instruction 0727
Early Childhood 0518
Elementary 0524
Finance 0277
Guidance and Counseling 0519
Health 0680
Higher 0745
History of 0520
Home Economics 0278
Industrial 0521
Language and Literature 0279
Mathematics 0280
Music 0522
Philosophy of 0998
Physical 0523

Psychology 0525
Reading 0535
Religious 0527
Sciences 0714
Secondary 0533
Social Sciences 0534
Sociology of 0340
Special 0529
Teacher Training 0530
Technology 0710
Tests and Measurements 0288
Vocational 0747

LANGUAGE, LITERATURE AND LINGUISTICS

Language 0679
General 0289
Ancient 0290
Linguistics 0291
Modern
Literature 0401
General 0294
Classical 0295
Comparative 0297
Medieval 0298
Modern 0316
African 0591
American 0305
Asian 0352
Canadian (English) 0355
Canadian (French) 0593
English 0311
Germanic 0312
Latin American 0315
Middle Eastern 0313
Romance 0314
Slavic and East European

PHILOSOPHY, RELIGION AND THEOLOGY

Philosophy 0422
Religion
General 0318
Biblical Studies 0321
Clergy 0319
History of 0320
Philosophy of 0322
Theology 0469

SOCIAL SCIENCES

American Studies 0323
Anthropology
Archaeology 0324
Cultural 0326
Physical 0327
Business Administration
General 0310
Accounting 0272
Banking 0770
Management 0454
Marketing 0338
Canadian Studies 0385
Economics
General 0501
Agricultural 0503
Commerce Business 0505
Finance 0508
History 0509
Labor 0510
Theory 0511
Folklore 0358
Geography 0366
Gerontology 0351
History
General 0578

Ancient 0579
Medieval 0581
Modern 0582
Black 0328
African 0331
Asia, Australia and Oceania 0332
Canadian 0334
European 0335
Latin American 0336
Middle Eastern 0333
United States 0337
History of Science 0585
Law 0398
Political Science
General 0615
International Law and Relations 0616
Public Administration 0617
Recreation 0814
Social Work 0452
Sociology
General 0626
Criminology and Penology 0627
Demography 0938
Ethnic and Racial Studies 0631
Individual and Family Studies 0628
Industrial and Labor Relations 0629
Public and Social Welfare 0630
Social Structure and Development 0700
Theory and Methods 0344
Transportation 0709
Urban and Regional Planning 0999
Women's Studies 0453

THE SCIENCES AND ENGINEERING

BIOLOGICAL SCIENCES

Agriculture
General 0473
Agronomy 0285
Animal Culture and Nutrition 0475
Animal Pathology 0476
Food Science and Technology 0359
Forestry and Wildlife 0478
Plant Culture 0479
Plant Pathology 0480
Plant Physiology 0817
Range Management 0777
Wood Technology 0746
Biology
General 0306
Anatomy 0287
Biostatistics 0308
Botany 0309
Cell 0379
Ecology 0329
Entomology 0353
Genetics 0369
Limnology 0793
Microbiology 0410
Molecular 0307
Neuroscience 0317
Oceanography 0416
Physiology 0433
Radiation 0821
Veterinary Science 0778
Zoology 0472
Biophysics
General 0786
Medical 0760
EARTH SCIENCES
Biogeochemistry 0425
Geochemistry 0996

Geodesy 0370
Geology 0372
Geophysics 0373
Hydrology 0388
Mineralogy 0411
Paleobotany 0345
Paleoecology 0426
Paleontology 0418
Paleozoology 0985
Palynology 0427
Physical Geography 0368
Physical Oceanography 0415

HEALTH AND ENVIRONMENTAL SCIENCES

Environmental Sciences 0768
Health Sciences
General 0566
Audiology 0300
Chemotherapy 0992
Dentistry 0567
Education 0350
Hospital Management 0769
Human Development 0758
Immunology 0982
Medicine and Surgery 0564
Mental Health 0347
Nursing 0569
Nutrition 0570
Obstetrics and Gynecology 0380
Occupational Health and Therapy 0354
Ophthalmology 0381
Pathology 0571
Pharmacology 0419
Pharmacy 0572
Physical Therapy 0382
Public Health 0573
Radiology 0574
Recreation 0575

Speech Pathology 0460
Toxicology 0383
Home Economics 0386

PHYSICAL SCIENCES

Pure Sciences
Chemistry
General 0485
Agricultural 0749
Analytical 0486
Biochemistry 0487
Inorganic 0488
Nuclear 0738
Organic 0490
Pharmaceutical 0491
Physical 0494
Polymer 0495
Radiation 0754
Mathematics 0405
Physics
General 0605
Acoustics 0986
Astronomy and Astrophysics 0606
Atmospheric Science 0608
Atomic 0748
Electronics and Electricity 0607
Elementary Particles and High Energy 0798
Fluid and Plasma 0759
Molecular 0609
Nuclear 0610
Optics 0752
Radiation 0756
Solid State 0611
Statistics 0463
Applied Sciences
Applied Mechanics 0346
Computer Science 0984

Engineering
General 0537
Aerospace 0538
Agricultural 0539
Automotive 0540
Biomedical 0541
Chemical 0542
Civil 0543
Electronics and Electrical 0544
Heat and Thermodynamics 0348
Hydraulic 0545
Industrial 0546
Marine 0547
Materials Science 0794
Mechanical 0548
Metallurgy 0743
Mining 0551
Nuclear 0552
Packaging 0549
Petroleum 0765
Sanitary and Municipal 0554
System Science 0790
Geotechnology 0428
Operations Research 0796
Plastics Technology 0795
Textile Technology 0994

PSYCHOLOGY

General 0621
Behavioral 0384
Clinical 0622
Developmental 0620
Experimental 0623
Industrial 0624
Personality 0625
Physiological 0989
Psychobiology 0349
Psychometrics 0632
Social 0451



TABLE OF CONTENTS

	Page
Table of Contents.....	iv
List of Tables.....	vi
List of Figures.....	vii
Abstract.....	xii
List of Abbreviations.....	xiii
Acknowledgements.....	xv
General Introduction.....	1
Chapter 1. Energetic Costs of Daily Activities in the Temperate Reef Fish (<u>Tautogolabrus</u> <u>adspersus</u>).	
Introduction.....	12
Methods.....	15
Results.....	24
Discussion.....	45
Chapter 2. Time and Energy Budgets of the Temperate Reef Fish (<u>Tautogolabrus</u> <u>adspersus</u>).	
Introduction.....	53
Methods.....	56
Results.....	60
Discussion.....	78

Chapter 3. Effects of Conspecific Density on Settlement, Growth and Post-settlement Mortality of a Temperate Reef Fish.

Introduction.....	92
Methods.....	95
Results.....	98
Discussion.....	113

Chapter 4. Effects of Habitat on Settlement, Growth and Post-settlement Mortality of a Temperate Reef Fish.

Introduction.....	117
Methods.....	121
Results.....	126
Discussion.....	152

Chapter 5. Intraspecific Variation in Growth and Metabolic Efficiency of Cunner (Tautogolabrus adspersus).

Introduction.....	161
Methods.....	164
Results.....	168
Discussion.....	187

Literature Cited.....	196
-----------------------	-----

LIST OF TABLES

Table 2.1. Energy budgets of (a) unfed and (b) fed 0+ cunner at three temperatures (5°C, 10°C and 15°C). The amount of energy (mg O ₂ kg ⁻¹ hr ⁻¹) allocated to each activity was calculated as the metabolic cost of each activity (determined in Chapter 1), multiplied by the proportion of time spent on each activity. Resting metabolism = standard metabolic rate from y intercepts of Fig. 1.2. Foraging costs were calculated as the time spent at a given swimming speed (Fig. 2.2) multiplied by the energetic cost of swimming at that speed (Fig. 1.2), plus SDA (difference in elevation of fed vs unfed regressions in Fig. 1.2). Defense costs are assumed to be 95% of the active metabolic rate (see Fig. 1.7). The total metabolic cost is also presented as a percentage of the metabolic scope for activity. n.d.: no data (fish did not feed at 5°C).....	66
Table 2.2. Time budgets of 0+ cunner inhabiting different habitat types. Water temperature was 15°C. The mean proportion of time (± 1 standard error) allocated to each activity was calculated from successive 2 hr observation periods.....	68
Table 2.3. Energy budgets of (a) unfed and (b) fed 0+ cunner inhabiting different habitat types. The amount of energy (mg O ₂ kg ⁻¹ hr ⁻¹) allocated to each activity was calculated as per Table 2.1.....	71
Table 2.4. Time budgets of 0+ cunner subjected to different conspecific density treatments. Observations were carried out on rocky reef habitats only. Water temperature was 15°C. The mean proportion of time allocated to each activity was calculated from successive 2 hr observation periods.....	72
Table 2.5. Energy budgets of (a) unfed and (b) fed 0+ cunner subjected to different conspecific density treatments. The amount of energy (mg O ₂ kg ⁻¹ hr ⁻¹) allocated to each activity was calculated as per Table 2.1.....	74
Table 4.1. Regression of capture success on substrate rugosity, juvenile survival, and post-recruitment density (recruitment success) in 1991 and 1992.....	149

LIST OF FIGURES

Figure 1.1. Oxygen consumption of fed and unfed 0+ cunner at (a) 10°C and (b) 15°C. Cunner were fed to satiation (200 mg of finely chopped shrimp) at time = 0 hrs. Swimming speed was maintained at 1.5 cm sec ⁻¹ . Vertical error bars represent ±1 standard deviation. Standard and active metabolic rates (see Fig. 1.3) are provided as a reference. The SDA elicited by this meal should approximate that caused by a natural diet, which is composed mainly of various small crustacea.....	26
Figure 1.2. The relationship between oxygen consumption and swimming speed for fed and unfed 0+ cunner at (a) 5°C, (b) 10°C, and (c) 15°C. 'Fed' fish were given 200 mg of finely chopped shrimp. Oxygen consumption was measured for 30 min at 1 cm sec ⁻¹ and at 5 cm sec ⁻¹ intervals from 5 cm sec ⁻¹ until the critical swimming speed was attained. The experiment was repeated 3 times on each of 5 individuals.....	29
Figure 1.3. Standard and active metabolic rates of fed and unfed 0+ cunner at three temperatures (5°C, 10°C and 15°C). Means were derived from triplicate runs on each of 5 individuals. Vertical error bars represent ±1 standard deviation.....	32
Figure 1.4. Critical swimming speed (body lengths sec ⁻¹) of fed and unfed 0+ cunner at three temperatures (5°C, 10°C and 15°C). Means were derived from triplicate runs on each of 5 individuals. Vertical error bars represent ±1 standard deviation.....	34
Figure 1.5. Scope for activity of fed and unfed 0+ cunner at three temperatures (5°C, 10°C and 15°C). Means were derived from triplicate runs on each of 5 individuals. Vertical error bars represent ±1 standard deviation.....	37
Figure 1.6. Oxygen consumption of unfed 0+ cunner during daytime rest and nocturnal torpor. Means were derived from triplicate runs on each of 5 individuals. Vertical error bars represent ±1 standard deviation.....	39

Figure 1.7. Oxygen consumption of groups of 3 unfed 0+ cunner presented with a range of shelter site availability. Data are presented relative to the sum of the active and standard metabolic rates of each individual within the group. Active = sum of individual active rates. Individual routine = sum of individual routine rates. Group routine = routine metabolic rate of a group of 3 cunner sharing the chamber. The experiment was conducted at (a) 5°C, (b) 10°C and (c) 15°C. Vertical error bars represent ± 1 standard deviation.....	42
Figure 1.8. The number of agonistic interactions (bites min^{-1}) between unfed 0+ cunner presented with a range of shelter site availability. The experiment was conducted at 5°C, 10°C and 15°C. Vertical error bars represent ± 1 standard deviation.....	44
Figure 2.1. Temporal change in time budgets (allocation of time to daily activities) of 0+ cunner from September 1 to December 15, 1991. The mean proportion of time (± 1 standard error) allocated to each activity was calculated from successive 2 hr observation periods. Data are plotted as a function of date and total length. Water temperature is also presented as a function of date.....	63
Figure 2.2. Three-dimensional plot of foraging speed (cm sec^{-1}) of 0+ cunner as a function of temperature and total length. Foraging speed was measured <u>in situ</u> by placing a rope grid over the substrate and counting the number of squares over which a fish swam per unit time.....	65
Figure 2.3. Diel time budget for 0+ cunner at 15°C, in rocky reef habitats. Proportion of time allocated to each activity is presented on an hourly basis for a representative 24 hr period. The mean proportion of time allocated to each activity was calculated from successive 2 hr observation periods. Vertical error bars represent ± 1 standard error.....	77
Figure 2.4. (a) Diel cycle of energy expenditure for 'unfed' 0+ cunner at 15°C, in August and September, 1992. Energetic cost (measured as oxygen consumption ($\text{mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$) of each activity) was calculated as per Table 2.1. (b) Diel energy expenditure expressed as a percentage of scope for activity.....	80

Figure 2.5. (a) Diel cycle of energy expenditure for 'fed' 0+ cunner at 15°C, in August and September, 1992. Energetic cost (measured as oxygen consumption ($\text{mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$) of each activity) was calculated as per Table 2.1. (b) Diel energy expenditure expressed as a percentage of scope for activity.....	82
Figure 3.1. Decline in population abundance of 0+ cunner from July through October, 1992, for each of three adult density manipulation treatments. Low density: adult density artificially reduced to 1 m^{-2} ; Control: adult density unmanipulated; High density: adult density artificially increased to 5 m^{-2} . Vertical error bars represent ± 1 standard deviation.....	100
Figure 3.2. Effects of adult conspecific density on (a) settlement, (b) post-settlement survival and (c) growth rate of 0+ cunner. Low density: adult density artificially reduced to 1 m^{-2} ; Control: adult density unmanipulated; High density: adult density artificially increased to 5 m^{-2} . Vertical error bars represent ± 1 standard deviation.....	102
Figure 3.3. Effects of rank size at settlement on (a) rank size at the end of September (i.e. post-recruitment size) and (b) rank growth rate of 0+ cunner. Tied ranks are averaged.....	105
Figure 3.4. Effects of size at settlement on percent post-settlement survival of 0+ cunner. Survival was calculated for each 1 mm size-class of settlers as the proportion of total settlers remaining in November. Data are for control reefs only.....	107
Figure 3.5. Decline in population abundance of 0+ cunner for each of three recruit density manipulation treatments. Low density: recruit density artificially reduced to 3 m^{-2} ; Control: recruit density unmanipulated; High density: recruit density artificially increased to 10 m^{-2} . Vertical error bars represent ± 1 standard deviation.....	110
Figure 3.6. Effects of conspecific recruit density on (a) post-settlement survival and (b) growth rate of 0+ cunner. Low density: recruit density artificially reduced to 3 m^{-2} ; Control: recruit density unmanipulated; High density: recruit density artificially increased to 10 m^{-2} . Vertical error bars represent ± 1 standard deviation.....	112

Figure 4.1. Among-habitat variation in population density of adult cunner at 3 sites in St. Margarets' Bay, Nova Scotia. Data are from censuses conducted at 10-day intervals from August to November, 1991 and 1992. Vertical error bars represent ± 1 standard deviation.....	128
Figure 4.2. Effects of substrate rugosity on population density of adult cunner in St. Margarets' Bay, Nova Scotia. Data are from censuses conducted at 10-day intervals from August to November, 1991 and 1992.....	131
Figure 4.3. Among-habitat variation in settlement of cunner at 3 sites in St. Margarets' Bay, Nova Scotia, in 1991 and 1992. Vertical error bars represent ± 1 standard deviation.....	133
Figure 4.4. Temporal variation in population density of resident 0+ cunner at 3 sites in St. Margarets' Bay, Nova Scotia, in 1991 and 1992, from censuses at 10-day intervals. Vertical error bars represent ± 1 standard deviation.....	135
Figure 4.5. Among-habitat variation in percent post-settlement survival of 0+ cunner at 3 sites in St. Margarets' Bay, Nova Scotia, in 1991 and 1992. Survival was calculated as the number of 0+ cunner remaining on a given transect in November, divided by the total number of cunner to settle on that transect. Vertical error bars represent ± 1 standard deviation.....	138
Figure 4.6. Effects of substrate rugosity on (a) post-settlement survival and (b) post-recruitment density of 0+ cunner in St. Margarets' Bay, Nova Scotia, in 1991 and 1992.....	140
Figure 4.7. Among-habitat variation in post-recruitment density of 0+ cunner at 3 sites in St. Margarets' Bay, Nova Scotia, in 1991 and 1992. Vertical error bars represent ± 1 standard deviation.....	142
Figure 4.8. Among-habitat variation in capture success of cottid predators feeding on 0+ cunner in St. Margarets' Bay, Nova Scotia, in 1991 and 1992. Data from all sites are pooled. Vertical error bars represent ± 1 standard deviation.....	146
Figure 4.9. Effects of substrate rugosity on capture success of cottid predators feeding on 0+ cunner in St. Margarets' Bay, Nova Scotia, in 1991 and 1992.....	148

Figure 4.10. Among-habitat variation in growth rate of 0+ cunner at 3 sites in St. Margarets' Bay, Nova Scotia, in 1991 and 1992. Vertical error bars represent ± 1 standard deviation.....	151
Figure 5.1. Variation in water temperature and the temporal increase in total length of 10 individual 0+ cunner at Back Cove Reef (determined by mark/recapture) from August 27 to Dec. 14, 1992.....	170
Figure 5.2. Effects of temperature on <u>in situ</u> growth rate of 10 individual 0+ cunner from Back Cove Reef. Growth rates were calculated from successive recaptures and measurements of marked individuals.....	173
Figure 5.3. The relationship between oxygen consumption and swimming speed of 10 individual 0+ cunner. Standard metabolic rates of each individual are extrapolated from the y intercept of the regression lines. The slope of each line represents the energetic cost of locomotion.....	175
Figure 5.4. Scope for activity of 10 individual 0+ cunner (3 repeated measures per individual) from Back Cove Reef. Vertical error bars represent ± 1 standard deviation.....	177
Figure 5.5. Oxygen consumption of unfed (control) individual 0+ cunner (3 repeated measures per individual) swimming at 1.5 cm s^{-1} . Vertical error bars represent ± 1 standard deviation.....	180
Figure 5.6. Oxygen consumption over a 24 hr time period for 10 individual 0+ cunner fed 200 mg of chopped shrimp at time = 0. Vertical error bars represent ± 1 standard deviation.....	182
Figure 5.7. Magnitude of apparent SDA for 10 individual 0+ cunner. (a) Absolute value of magnitude. (b) Magnitude of SDA as a percentage of scope for activity (magnitude of SDA over a 12 hr duration was divided by aerobic scope over same period, i.e. magnitude of SDA / (aerobic scope x 12)). Vertical error bars represent ± 1 standard deviation.....	184
Figure 5.8. Relationship of growth rate of 10 individual 0+ cunner to (a) absolute scope for activity, and (b) metabolic cost of foraging (i.e. magnitude of SDA) as a percentage of scope for activity. Growth rate was calculated as the mean increase in length (mm day^{-1}) over the previous summer (see Fig. 5.1).....	186

ABSTRACT

This study examines the role of energy as a limiting resource in the regulation of demersal juvenile fish populations. In situ time and energy budgets of daily activities were constructed for cunner (Tautogolabrus adspersus), a common temperate reef fish, in St. Margarets Bay, NS. Maximum O₂ consumption of each component of the daily energy budget (resting, foraging and shelter site defense) can sum to a value much higher than the maximum O₂ uptake. Cunner must therefore allocate energy to each component so that the scope for activity is not exceeded. Under natural conditions, cunner operated at a low proportion of their scope for activity, although a peak of activity late in the day substantially reduced surplus power. Competition for shelter sites was an important component of the energy budget of cunner and could expend almost the entire scope for activity when shelter was limiting. This greatly reduced the surplus energy for growth, as evidenced by the strong density-dependence of growth measured in populations where density had been manipulated by transplanting fish among isolated reefs. High densities of conspecifics also reduced post-settlement survival, although density had no effect on settlement rate. Thus it appears that post-settlement processes involving resource (energy) limitation are more important than settlement variation in regulating populations of cunner in St. Margarets Bay.

No particular energetic advantage was offered by any of 4 available habitat types (reef, cobble, seagrass, sand), and cunner showed no evidence of microhabitat selection at or following settlement. Instead, differential predation pressure resulted in variation of recruitment success among habitats. Predators were less successful at capturing newly settled cunner in topographically complex habitats (reef and cobble), and survival was highest in those habitats. Growth rates of 0+ cunner also differed among habitats but was highest in seagrass beds. Thus, 0+ cunner face trade-offs between energy gain (growth) and predation mortality. Mortality of cunner was size-dependent and growth rates of individual fish may therefore be good predictors of their potential survival. Individual growth rates were correlated with the scope for activity remaining after the metabolic costs of foraging were met. Thus, genetic techniques that focus on the heritability of growth processes might be useful predictors of survival of juvenile demersal fishes.

LIST OF ABBREVIATIONS

AMR	active metabolic rate
ANOVA	analysis of variance
bl	body lengths
°C	degrees Celsius
cm	centimetres
E_d	energy allocated to shelter site defense
E_f	energy allocated to foraging
E_r	energy allocated to rest (standard metabolic rate)
E_{tot}	total energy expenditure
Fig.	Figure
g	grams
hr	hours
kg	kilograms
kJ	kiloJoules
L	litres
m	metres
mg	milligrams
min	minutes
ml	millilitres
mm	millimetres

O_2	oxygen
p	probability
R	total aerobic metabolism
R_a	activity metabolism
R_f	apparent specific dynamic action
R_s	standard metabolic rate
sec	seconds
s.d.	standard deviation from the mean
SDA	specific dynamic action
S.E.	standard error of the mean
SMR	standard metabolic rate
T	temperature
T_d	time allocated to shelter site defense
T_f	time allocated to foraging
T_r	time allocated to resting (period of inactivity)
T_{tot}	total time expenditure
U_{crit}	critical (maximum sustainable) swimming speed
VO_2	rate of oxygen uptake
VO_{2max}	maximum rate of oxygen uptake (= active metabolic rate)

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to my supervisor, Dr. R. G. Boutilier, not only for teaching me so much about physiology and biology in general, but for his own willingness to learn new fields. Dr. Boutilier's broad-minded approach to student supervision made this interdisciplinary research possible, and resulted in a much more integrated thesis than I might otherwise have written.

I would also like to thank my committee members, Dr. A. Pinder and Dr. S. R. Kerr, for reviewing my work and for providing many helpful comments along the way, and Dr. R. O'Dor generously provided me with the Orion oxygen electrode. Dale Webber kindly supplied expert advice on the respirometry setup. Chapter 4 benefited from discussions of cunner-habitat interactions with Dr. P. Levin of the University of North Carolina. The thesis as a whole greatly benefited from discussions of predation and foraging with Dr. F. Juanes of the University of Massachusetts. Thanks also go to several people in the Department who helped out at times and generally made life easier: Dr. Tom Miyake, Nancy Irwin, Todd Bishop, and Danny Jackson (thanks for the equipment loan).

I would like to extend special thanks to my parents, who always encouraged my curiosity and my love of the oceans. I would especially like to thank my father, Dr. B. O. J. Tupper, for his continued support of my academic career. Lastly, I would like to express my deepest gratitude to my wife, Dr. Ione Hunt von Herbing, for her love and support in all aspects of our lives, scientific and otherwise, as well as for being my sounding board for the past seven years.

Funding for this study was provided by an operating grant from the Ocean Production Enhancement Network to Dr. R. G. Boutilier and Dr. S. R. Kerr, an operating grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) to Dr. R. G. Boutilier, and by an NSERC Post-graduate Scholarship and a Dalhousie Graduate Scholarship to MT.

GENERAL INTRODUCTION

Variability in the survival of early life history stages of fish is proposed to be a major factor limiting the size of adult populations. While studies of recruitment variability have focused largely on survival of planktonic larvae, recent evidence has pointed to early juvenile survivorship as an important contributor to year-class strength (Malloy and Targett 1991). Early post-settlement survival may be affected by predation, competition, growth, activity and behaviour (Jones 1991). However, little is known about the processes regulating settlement, growth and survival of age 0+ (first-year juvenile) fish in temperate marine ecosystems. In particular, little is known of the early juvenile stages of the cunner (Tautogolabrus adspersus), one of the most common inshore species from Newfoundland to Delaware, and a major component of the tidal and marine recreational fishery throughout its range.

Settlement ecology and habitat selection

One of the major determinants of settlement and post-settlement mortality of fish is the availability of shelter (Luckhurst and Luckhurst 1978, Shulman 1985a, Connell and Jones 1991, Levin 1991). Adequate protection from predation is considered an important characteristic of nursery habitats (Shulman 1984, McFarland et al. 1985); habitats characterised by high substrate complexity should therefore favour post-settlement survival through decreased predation pressure (Mattila 1992). Lough et al. (1989)

observed that pelagic stages of Atlantic cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) were widespread across Georges' Bank in late spring, but by late July demersal juveniles were abundant only on pebble/gravel deposits and almost absent from sand bottoms. They hypothesized that the pebble/gravel habitat favoured post-recruitment survival through predator avoidance and that the presence of pebble/gravel deposits on northeastern Georges' Bank might be essential to the recruitment success of local gadid populations. Levin (1991) found that the abundance of newly settled cunner was positively associated with macrophyte cover and negatively associated with low-complexity habitats. Competition for limited resources, particularly food (Jones 1986) and shelter (Shulman 1984, 1985a), forms the basis of the "resource-limitation model" of fish population dynamics. This model predicts that due to density-dependent post-settlement processes such as competition and predation, population densities of fish in a given habitat will remain relatively constant throughout time, at or near the carrying capacity of the habitat (Mapstone and Fowler 1988). Thus, settlement, growth and mortality of 0+ cunner will depend on either the population density of conspecifics (e.g. Jones 1987), or the population density of competitor species (e.g. Shulman 1985b). The opposing "recruitment-limitation" model argues that despite the prodigious fecundity of many marine fishes, stochastic planktonic processes limit the number of larvae available for settlement to coastal areas (Doherty 1982, 1983; Victor 1983, 1986; Milicich et al. 1992; Doherty and Fowler 1994). The model predicts, therefore, that the population density of fish in a given habitat will vary both spatially and temporally (Mapstone and Fowler 1988), and that settlement, growth and mortality will

be independent of population density. Recent research suggests that these theories are not mutually exclusive; i.e. populations are limited by both pre-settlement and post-settlement processes (Doherty and Williams 1988; Warner and Hughes 1988; Jones 1990, 1991; Hixon and Beets 1993; Doherty and Fowler 1994; Levin 1994a).

In temperate marine ecosystems, temperature is a key factor controlling behaviour, activity and growth and can have a profound effect on the first-year survival of juvenile fish (Shuter et al. 1980). Extreme temperatures may limit the growth of an organism and its scope for activity, making it more vulnerable to predation and competition. For example, sand smelt (Atherina boyeri) do not feed at temperatures below 10°C, and their maximum sustained swimming speed is markedly reduced below 7°C (Henderson et al. 1988). Thus, sand smelt do not feed throughout winter, but survive on stored lipids, and overwinter survival is generally much higher in larger individuals (Henderson et al. 1988). Faster growth during the first several months may therefore be an advantage to young-of-year fish (Walsh 1987). Like sand smelt, the metabolic rate of cunner is markedly depressed by falling temperatures (Hauggaard and Irving 1947). Cunner become torpid as water temperatures fall below 6-8°C, and remain dormant in their shelter sites over winter (Auster 1989). Lack of suitable shelter at this time may result in mortality either through predation or by the fish freezing upon contact with ice crystals in the water (Goddard et al. 1992). Thus, the interactive effects of environmental variables (particularly temperature, but also salinity and dissolved oxygen), shelter availability and prey density may result in a restriction of the carrying capacity of a nearshore habitat, limiting the population size of resident fishes. Coutant and Benson (1985) found that the thickness

of suitable water column (where $T < 29^{\circ}\text{C}$ and $[\text{O}_2] > 2 \text{ mg ml}^{-1}$) in Chesapeake Bay was significantly correlated with the abundance of juvenile striped bass (Morone saxatilis) the following year. However, for years when the thickness of suitable water column was greater than 18 m, juvenile abundance indices for the following year ranged widely. These results suggest that the availability of suitable habitat may limit population size and reproductive success of striped bass; at these times the population is resource-limited. At other times, when habitat is not limiting, population size of this species is more likely to be limited by recruitment, due to stochastic larval survival in the plankton. Note that resource-limitation in this case can be viewed from two perspectives. First, the habitat itself can be considered the resource - less suitable habitat will support fewer fish. Second, energy can be considered the limiting resource. Outside the environmental preferenda, energy is directed away from growth and gamete production as the cost of standard (or routine) metabolism increases. Thus, the population is limited by the energetic costs of survival in a suboptimal habitat.

On the Atlantic coast of Canada, juvenile cunner settle in shallow nearshore habitats which can be exposed to temperatures of $> 20^{\circ}\text{C}$ in late summer and $< 0^{\circ}\text{C}$ in winter (MacDonald et al. 1985, Scott and Scott 1988). These extremes of temperature may force 0+ cunner to remain dormant for 4-5 months of the year. In order to survive their first winter, cunner must secure a shelter site (Dew 1976) and must accumulate sufficient energy stores to support the metabolic rate during dormancy. Moreover, cunner must reach a certain minimum body size in order to be able to spawn the next summer (Dew 1976). If shelter sites are in limited supply, individuals may compete for overwintering

refuge. However, too much time spent defending shelter sites may be energetically costly. Sufficient foraging must occur to maximize body size and winter energy reserves, thus ensuring overwinter survival and the ability to spawn by the next summer. If cunner do not attain the required size by their second summer, they will not spawn until the following summer. In a species with a reproductive span of 4-5 years, the loss of a spawning season may result in a serious reduction in lifetime fitness.

Energetics of activity and growth

Individual organisms must allocate limited resources in a fashion that favours their genetic representation in future generations, i.e. in a way that optimizes the fitness of the individual (Sibly and Calow 1986; Wootton 1990). Energy can be considered a finite resource limiting the growth and survival of an individual or population. Maintenance and growth of organisms requires that energy be directed to foraging and processing of nutrients. Survival, however, may rely on energy being allocated to other activities, such as shelter site defense or predator evasion. Intraspecific differences in the energetic cost of feeding, locomotion and growth may result in differential survival of juvenile fish, thereby transmitting the genes for efficient energy metabolism to future populations (Arnold 1988).

Aerobic metabolic scope

One energetic measurement that may be useful as an index of fitness is the aerobic metabolic scope, or "scope for activity" (Fry 1947). Aerobic scope is defined as the difference between the active metabolic rate (oxygen consumption per unit time of an animal swimming at its maximum sustainable velocity) and the standard metabolic rate (oxygen consumption per unit time of an unfed animal at rest, i.e. holding its position in still water). It follows that the greater this difference, the greater the available energy for feeding and digestion, osmoregulation and active behaviours such as foraging, migration, territorial defence, courtship behaviour, etc. Differences in aerobic scope between individuals, populations or species may translate into differences in foraging/migration range, growth rate, and reproductive success (Beamish and Trippel 1990). In the case of juvenile fish, the major components of the energy budget may be the metabolic costs of feeding, locomotion and shelter site defense, as much of a young fishes' time is likely spent on foraging, growth, and predator evasion.

Apparent Specific Dynamic Action

Apparent specific dynamic action (SDA) is a measure of the energetic costs of feeding and growth (i.e. ingestion, digestion and absorption of food). SDA is characteristically observed as a postprandial increase in oxygen consumption of the fish, resulting in a temporary reduction in aerobic scope. This reduction in the scope for

activity may limit further foraging and may place the fish at a greater risk of predation or competitive exclusion (Vahl and Davenport 1979). Various environmental factors may influence the amplitude, magnitude and/or duration of the SDA. These include temperature, oxygen concentration, and stage of development (i.e. larval, juvenile or adult; Jobling 1981). Information about the variation of SDA between individuals, populations or species might be used to predict foraging patterns among these units. For example, a high SDA might limit further foraging by reducing the aerobic scope (i.e. allocation of energy to digestion means a reduction of energy for locomotion). This could result in more intermittent and confined foraging, compared to a fish exhibiting low SDA, where one might predict greater cruising endurance and therefore a wider foraging range. Thus, differences in the magnitude of SDA may act to optimize or constrain the scope for activity. For example, an individual with high SDA may optimize its foraging ability by feeding in areas of fairly uniform prey distribution and density, whereas an individual with low SDA may be more successful than the former in an area of spatially patchy prey.

Soofiani and Hawkins (1982) reported that oxygen consumption due to apparent SDA could rise to as much as 98% of the active metabolic rate of juvenile North Sea cod (Gadus morhua) fed to satiation. In comparison, feeding to satiation reduced the scope for activity by 50% in the largemouth bass (Micropterus salmoides; Beamish 1974), by 50% in the blenny (Blennius pholis; Vahl and Davenport 1979) and by 30-40% in the aholehole (Kuhlia sandvicensis; Muir and Niimi 1972). Salmonids are thought to retain an even larger proportion of their aerobic scope after feeding (Soofiani and Hawkins

1982), although Paloheimo and Dickie (1966) reported that SDA could rise to 100% of the active metabolic rate. Tagging studies on juvenile North Sea cod (Hawkins et al. 1974, 1980) suggest that swimming speeds of these fish were "so low that the proportion of the energy budget attributable to swimming is almost negligible" (Soofiani and Priede 1985, p. 128). However, it should be noted that it is extremely difficult to obtain accurate estimates of fish swimming speed using this tagging method, and energy expenditure is generally underestimated by the mean swimming speed obtained (Björnsson 1985). Soofiani and Priede (1985) state that their values of SDA in juvenile North Sea cod actually exceed active aerobic metabolic rates, leaving absolutely no scope for activity. However, the value of this study is questionable given that Soofiani and Priede's measure of active metabolic rate was the maximum level of oxygen consumption observed during the post-exercise period, not at the maximum sustainable velocity (see Tang et al. 1994).

In many species of demersal fish, growth depensation (an increase in the variance of size at a given age) occurs within populations of juveniles (e.g. Forrester 1990). Variation in growth rates of individuals can occur through differential access to prey, but might also be linked to heritable differences in scope for activity (greater scope equals more energy for foraging) or SDA (lower cost of feeding means more food can be processed per unit energy). Alternatively, high SDA might be mechanistically linked to high growth rate through more rapid assimilation of food. If so, growth rate and SDA would be positively correlated.

Environmental dependence of aerobic scope and SDA

In nature, the allocation of energy to growth and activity takes place in a dynamic environment (Wootton 1990). This environmental variability may entail temporal or spatial variation in abiotic factors (e.g. temperature), as well as biotic factors (e.g. conspecific density, prey availability, or predation risk). Thus, a central problem in the study of ecological energetics is to determine the responses of individual organisms (in terms of allocation of energy and time) to changes in the environment (Wootton 1990).

The scope for activity and the effect it might have on predictions of foraging and territorial behaviours of individuals or populations of age 0+ cunner could change markedly if there were heritable differences in, for example, the thermal dependence of standard or active metabolism or SDA. As mentioned previously, age 0+ cunner along the northwest Atlantic coast move into shallow bays in the summer, encountering temperatures of greater than 20°C. Crawshaw et al (1981) suggested that young-of-year fish typically select warm, shallow water not only to avoid predation by larger fish, but because the increase in standard metabolic rates, coupled with a large food supply, permit more rapid growth. Paul et al. (1990) found that routine metabolic rates of unfed yellowfin sole (Limanda aspera) increased by 33% for every 1°C increase in water temperature. Conversely, larval fishes spawned during fall and winter in offshore North Carolina waters experienced a decrease in both temperature and salinity as they entered estuarine nursery areas (Hoss et al. 1988). The feeding, growth and routine metabolic rate of larval spot (Leiostomus xanthurus) and Atlantic croaker (Micropogonias undulatus)

declined as temperature dropped from 20°C to 10°C. While some metabolic compensation is possible when adapting to a new temperature regime (Hochachka and Somero 1984), maximum sustained swimming speeds, active metabolic rates and aerobic scope generally tend to decline with temperature (Dunn, 1987). As temperatures fall, decreasing rates of enzyme-catalysed reactions limit the amount of energy (in the form of ATP) that can be produced (Hochachka and Somero 1984; Dunn 1987). This is particularly true during acute temperature changes when underlying thermal compensation mechanisms are slow to adapt.

Soofiani and Hawkins (1982) found that for a ration of fixed size, SDA of juvenile North Sea cod generally increased with temperature. If, however, the temperature-dependent increase in SDA is greater than the increase in active metabolic rate, a decrease in aerobic scope may occur with increasing temperature.

Summary

Variation in first-year survival of juvenile fishes can be attributed to three major factors: (1) variable survival of planktonic larvae (outside the scope of this thesis), (2) availability of shelter for newly settled fish, and (3) variation in the energetic cost of feeding, activity and growth. These factors may be strongly influenced by abiotic variables (particularly temperature, but also salinity, dissolved oxygen and current speed) and by biotic variables (predation rates, competition, prey density). In order to predict year class strength of fish populations, detailed information must be gathered on rate of

recruitment to the population (i.e. settlement), individual rate of growth, and rate of mortality. In addition, energetics of feeding, activity (foraging, territorial defence, etc.) and growth must be elucidated and the effects of environmental variation accounted for. The purpose of this thesis is to determine the ecological and energetic variables influencing the distribution, growth and survival of age 0+ cunner, Tautogolabrus adspersus. Specifically, five problems are addressed. First, what are the metabolic costs of the major daily activities of cunner (resting, swimming, feeding, shelter site defense) and what are the effects of temperature on these costs? Second, what is the in situ allocation of time and energy to these activities, and how does this vary with abiotic and biotic factors such as habitat structure, population density, temperature and size/age? Third, what are the effects of intraspecific competition on settlement, growth and mortality of 0+ cunner? Fourth, what influence do environmental (habitat) variables such as availability of shelter and predation risk have on the settlement, growth and mortality of 0+ cunner? Finally, are there any direct relationships between individual patterns of energy allocation and growth and survival of individuals?

CHAPTER 1

ENERGETIC COSTS OF DAILY ACTIVITIES IN THE TEMPERATE REEF FISH (TAUTOGOLABRUS ADSPERSUS)

INTRODUCTION

Animals in their natural environment engage in various activities requiring large expenditures of energy over extended periods of time. As a result, animals routinely consume oxygen at rates well above resting levels. Studies of fish energetics have generally separated aerobic metabolism into three compartments:

$$R = R_s + R_f + R_a$$

(e.g. Priede 1985) where R is the total aerobic metabolism, R_s is the standard metabolic rate, R_f is the apparent specific dynamic action or SDA (also known as the apparent heat increment, see Beamish and Trippel 1990), and R_a is the activity metabolism (i.e. the oxygen consumption associated with locomotion). The standard metabolic rate is defined as the oxygen consumption per unit time of an unstressed, unfed fish in a resting state (Fry 1947). This is considered to be the minimum rate of respiratory metabolism (Furnell 1986). The maximum or "active" metabolic rate is measured as the oxygen consumption per unit time of a fish swimming at its maximum sustainable velocity (also known as the

critical swimming speed or U_{crit}). The difference between the active and standard metabolic rates is the aerobic metabolic scope or "scope for activity" (Fry 1947). The larger the scope for activity, the greater the available energy for maintenance functions such as feeding and digestion, growth and development, osmoregulation, and for active behaviours such as foraging, migration, territorial defense, and reproductive behaviours.

Apparent SDA is a measure of the energy expenditure associated with feeding and includes the energetic costs of ingestion, digestion and assimilation, but is primarily associated with protein metabolism (Jobling 1981). Apparent SDA is observed as a postprandial elevation of the rate of oxygen consumption, with a concomitant decrease in aerobic metabolic scope. The amplitude and duration of apparent SDA vary with species and with ration size, ration quality and temperature (Muir and Niimi 1972; Vahl and Davenport 1979). In most species, apparent SDA ranges from 1.5 to 2.5 times the standard metabolic rate (Jobling 1981). Soofiani and Hawkins (1982) reported that apparent SDA could be as large as the entire scope for activity in Atlantic cod (Gadus morhua). Other studies have found apparent SDA to be as large as 30-50% of the scope for activity (Muir and Niimi 1972; Beamish 1974; Vahl and Davenport 1979).

As with apparent SDA, activity metabolism can also account for a large proportion of the scope for activity (Brett and Groves 1979). Thus, when each of the components R_s , R_f and R_a is determined separately, the sum of the components may exceed the active metabolic rate (Brett and Groves 1979; Soofiani and Hawkins 1982; Soofiani and Priede 1985), i.e. $R_f + R_a$ may exceed the scope for activity. Over the short term, anaerobic metabolism may supply the extra energy needed, but this means that the animal incurs

an oxygen debt which must be repaid later (Brett 1964; Furnell 1986). Assuming that active metabolic rate is relatively constant for an individual, allocation of sustainable energy expenditure between R_f and R_a must occur within the limitations set by the active metabolic rate (Wootton 1990). The allocation of energy between standard metabolism, apparent SDA, and various activities has profound implications for the growth, survival and reproductive success of fish. Field studies of the swimming and feeding rates of brown trout (Salmo trutta) and Atlantic cod (Gadus morhua) indicate that fishes swim and feed below maximal rates and are thus routinely operating well below their maximum capacities (Priede 1985). Indeed, Priede (1985) suggests that the probability of dying increases as routine metabolism approaches the active or standard metabolic rates, i.e. at the upper and lower limits of the scope for activity. Thus, a fish should regulate its feeding and activity to meet its maintenance requirements, while maintaining a low probability of exceeding the scope for activity. The energy saved by a fish operating at a low power output can be allocated to growth or gamete production (Koch and Wieser 1983; Roff 1983), thus increasing the evolutionary fitness of the individual.

Variation in the abiotic environment may greatly influence patterns of energy allocation. Responses of fish to environmental change generally involve changes in the three components of metabolism, R_s , R_f and R_a , and in the scope for activity (Priede 1985; Wootton 1990). At higher latitudes, temperature is the most important factor affecting metabolic rates of fish. In general, extremes of temperature tend to decrease the scope for activity (Brett 1964; Elliott 1976). Fish should therefore display a preference for the temperature that maximizes their scope for activity; outside this preferendum, patterns of

energy allocation may change in order to minimize the reduction in scope for activity.

The purpose of this chapter is (1) to investigate the metabolic costs of feeding (R_f) and activity (R_a) in relation to scope for activity in the temperate reef fish, Tautogolabrus adspersus, and (2) to determine the effect of temperature on R_f , R_a and scope for activity.

METHODS

Study Species

The cunner, Tautogolabrus adspersus (fam. Labridae) inhabits nearshore waters from Conception Bay, Newfoundland, south to Delaware (Auster 1989). Cunner are most abundant from the low tide mark to a depth of about 18-30 m. They are strongly associated with cover, and are found in abundance around rocky reefs, wharves and pilings or in dense vegetation. Cunner have a restricted home range, and juveniles (age 0+) rarely move more than a few metres from their home shelter site (see Chapters 3 and 4).

The cunner is a diurnally active species that undergoes a nocturnal dormant, or torpid, state. Dormancy begins 5-55 min prior to sunset and ceases 16-41 min after sunrise (Olla et al. 1979). Cunner will normally secure themselves in their home shelter site before entering dormancy. If shelter is unavailable before nightfall, cunner will enter dormancy on open bottom, thereby greatly increasing their risk of mortality (Dew 1976). Cunner can survive a wide range of temperatures, but below 5°C cunner become torpid and their

oxygen consumption is depressed (Hauggaard and Irving 1943). During the winter months, cunner remain torpid within their home shelter site and do not feed. Activity resumes the next spring, when water temperatures reach 5-6°C.

Experimental protocol

Young-of-year cunner from St. Margarets Bay, Nova Scotia were collected from shallow reef habitats in August, 1991, using anaesthetic (10% solution of quinaldine sulfate (Sigma) in seawater). While cunners do not possess functional stomachs (Chao 1972), the intestine may act as a food storage organ (Levin 1994b). Guts of cunner sacrificed 2 weeks after capture and subsequent starvation still contained hard body part remains of small crustacea. Although these exoskeletal remains were probably indigestible and therefore unlikely to contribute significantly to SDA, all cunner were starved for 4 weeks prior to experiments, which were performed under conditions of constant light (Vahl and Davenport 1979). Cunner held without feeding tended to remain dormant for much of the time at all temperatures, and no significant gain or loss of mass was recorded between any of the temperature treatments. All individuals were subjected to experimental procedures at 5°C, 10°C and 15°C; cunner were acclimated to each temperature for 4 weeks prior to experimentation.

The respirometry system used for all experiments in this study consisted of two identical transparent plastic containers. Each of the circular 2.5 L containers could be sealed with gas-tight lids and were placed in a flowing-seawater bath, the temperature of

which was regulated to within $\pm 1^\circ\text{C}$ of each experimental temperature. Grids of 1 cm squares were drawn on the bottom of the containers, allowing swimming speeds of spontaneously active fish to be measured. The water bath rested on two magnetic stir plates; stir bars on the container bottoms provided a circular water flow, which could be regulated from 1-20 cm s^{-1} . Flow speed was calibrated by filming dye particles at given settings of the stir plate. Flow speed was measured about 2 cm from the outside edge of the container; this was where cunner appeared to prefer to hold station. Before measuring flow, the stir plate was run at a constant setting for 10 min; after which it ran at a more constant speed. Oxygen consumption was measured with an Orion oxygen probe (model 08-97-00), which was inserted through a hole in the container lid. A rubber stopper with the centre drilled out was placed around the neck of the probe and smeared with silicone grease. This ensured a gas-tight seal between the probe and the lid. The temperature of the water bath could be adjusted by varying the flow of cold water through the bath. Experiments were performed when ambient water temperatures matched the desired experimental temperature, in order to reduce the possibility of wide fluctuations ($> \pm 1^\circ\text{C}$) in temperature.

Experiment 1. Amplitude and duration of apparent SDA

The amplitude and duration of apparent SDA were measured for 5 individual young-of-year cunner (36-49 mm total length; 3.2-3.5 g wet weight). In each run, a cunner was placed in each of the two respirometer chambers, which was set at a flow

speed of 1 cm s^{-1} . The fish were left overnight to allow them to adjust to the chamber. In order to standardize the effects of feeding on metabolic rate, a pilot experiment was undertaken to assess the maximum ration that all 5 individuals would accept directly after 4 weeks starvation. The results of this experiment indicated that a ration of 0.2 g of shrimp satiated 4 of the 5 individuals. This ration did not change with temperature, suggesting that satiation was generally a function of meal size relative to gut volume. After the fish had acclimated to the chamber, 0.2 g of finely chopped shrimp suspended in seawater was pipetted into one chamber through a hole in the lid. The fish in the second chamber was not fed. The oxygen probe was inserted into the first chamber, and the decline in oxygen tension over a 30 min period was measured hourly at 0-6 hrs and thereafter at 8, 10, 12, 16, and 24 hours post-feeding. The fish was then removed from the respirometer and weighed. The oxygen probe was then transferred to the second chamber, and the oxygen consumption of the unfed fish was measured according to the same schedule. All 5 individuals were subjected to both fed and unfed runs, with a 2 week starvation and acclimation period between fed and unfed runs. After each individual had been subjected to both fed and unfed runs, it was fed ad libitum for one week before beginning the 4 week acclimation and starvation period prior to the next temperature treatment. The experiment was repeated on the same 5 fish at each temperature.

Experiment 2. Allocation of energy to feeding and locomotion

The standard and active metabolic rate and scope for activity were determined for the

same 5 individual cunner used in experiment 1. Individual unfed fish were placed in the respirometer chamber at a flow speed of 1 cm s^{-1} and left overnight (16 h) to adjust to the chamber and the flow. Oxygen consumption was then measured in 30 min runs over a range of incrementally increased swimming speeds. Cunner swam well in the respirometer, and preferred to hold station about 2 cm from the outside edge of the chamber, where they could remain more or less parallel to the water flow. At low swimming speeds, cunner employed a labriform mode of swimming, i.e. sculling with the pectoral fins. As swimming speeds increased, cunner gradually switched to a carangiform swimming mode, utilizing their trunk and tail musculature. When the fish could no longer hold station against the current, the experiment was terminated, and the fish was removed from the respirometer and weighed. The respirometer chambers were emptied and refilled after each run. Each individual underwent the procedure three times, with a 2 week rest between runs on the same individual. Oxygen consumption was regressed on swimming speed for each individual; the resulting equations were used to calculate the active metabolic rate, i.e. the oxygen consumption at the critical swimming speed (determined as per Brett 1964) and to extrapolate the standard metabolic rate, i.e. the oxygen consumption at the y intercept of the equation. Scope for activity was calculated as the difference between active and standard metabolic rates.

After all individuals had undergone the above procedure three times, the experiment was repeated on the same individuals, with the exception that each individual was fed 2 hr prior to beginning the run. The purpose of the 2 hr delay was to reduce the possibility of fish regurgitating the meal (Furnell 1986), which was never observed. The intent of

this stage of the experimental series was to introduce a second metabolic load (apparent SDA) to individuals already challenged by enforced activity. Both stages of this experiment were repeated on the same 5 individuals at 5°C, 10°C, and 15°C.

Experiment 3. Diurnal and seasonal variation in standard metabolism.

Cunner are nocturnally dormant year-round, and remain torpid over winter at temperatures < 5°C, although they will respond sluggishly if disturbed (Wicklund 1970). To determine if standard metabolism varied significantly between the dormant and active states, we measured oxygen consumption of individual cunner left in the respirometer overnight. The laboratory remained unlit, and black plastic was placed around the respirometer to ensure total darkness in the chamber. Two shelter sites (see Experiment 4 below) were placed in the chamber. An individual cunner was introduced to the chamber and was given 6 hr to adjust and enter the dormant state (this usually took < 2 hr, and all fish were always dormant before 6 hr). The respirometer was then sealed and recording of oxygen consumption started. The resulting measure of oxygen consumption was compared to rates of standard metabolism measured in experiment 2. This experiment was repeated three times (September, November and January) on each of the same 5 individuals used in the previous experiments, and was performed at 5°C, 10°C, and 15°C.

Experiment 4. Metabolic cost of shelter site defense

Individual cunner of nearly identical size (45 ± 4.9 mm total length; 5.0 ± 0.7 g wet weight) were used in this experiment. The standard and active metabolic rates and scopes for activity of these individuals were determined as per experiment 1. In further experiments, shelter sites for young-of-year cunner were constructed by cutting PVC pipe into 10 cm lengths of 2 cm internal diameter. Routine rates of oxygen consumption during 2 hr bouts of spontaneous activity were measured for each individual (3 runs per individual at 24 hr intervals; fish remained in the chamber between runs) with 1 shelter site present, and for a group of 3 individuals with 0, 1, 2, 3, or 4 shelter sites placed in the respirometer chamber. The bottom of the respirometer chamber encompassed an area of approximately 300 cm^2 (not including surface area provided by shelter sites). This approximated a density of 10 0+ individuals m^2 , which can occur in very dense natural populations (P. Nitzsche, Univ. of Massachusetts, pers. comm.). Each treatment was repeated in triplicate, with a 3 day interval between treatments. For each treatment the total oxygen consumption of the group was compared to the sum of the individual oxygen consumptions of the fish making up the group. If the group oxygen consumption exceeded the sum of the individual routine metabolic rates, it was assumed that the increased oxygen consumption resulted from interactions between individual cunner within the group. In order to support this assumption, behaviour of the group was observed throughout each run, and the number of agonistic interactions over shelter sites was recorded. As with the previous experiments, experiment 4 was conducted at 5°C ,

10°C, and 15°C.

Analysis of data

Prior to analyses, all numeric data were tested for normality using graphical probability plots (SYSTAT; Wilkinson 1990) and for homogeneity of variance using Bartlett's Test.

Experiment 1

Maximum amplitude (maximum postprandial VO_2) and duration of apparent SDA were compared between temperatures using independent t-tests, with temperature as a grouping variable (Wilkinson 1990). The duration was defined as the point at which the fed and unfed oxygen consumptions no longer differed significantly ($p > 0.05$). The magnitude of SDA was calculated for each run by averaging the amplitude between two successive points on the oxygen consumption curve and multiplying the average amplitude over starved fish (Δy) by the time separating the two points (Δx). The area under each successive pair of points was calculated in this fashion; the sum of these areas, i.e. the total area under the curve, represented the magnitude of apparent SDA. Magnitude of SDA was compared between temperature treatments using independent t-tests as above.

Experiment 2

To determine the effects of temperature and feeding on activity metabolism, oxygen consumption data from all repeats on the 5 individual cunner were pooled within treatments and regressed on swimming speed. Differences in the elevation and slope of these regressions between fed and unfed fish at a given temperature, and differences between temperatures in fish of the same digestive state, were determined by t-tests between slopes (Zar 1984). An increase in elevation of the regression line in fed fish over unfed fish would represent apparent SDA. A difference in slope between digestive states or between temperatures may indicate variation in the efficiency of locomotion, i.e. a difference in the amount of energy required for swimming at a given speed. Where more than two temperature treatments were compared, the experiment-wise error rate (Sokal and Rohlf 1981) was applied to the probability values of the t-test between slopes.

Differences in critical swimming speed, maximum sustainable oxygen consumption (VO_{2max}) and scope for activity were compared between fed and unfed fish using independent t-tests, and between temperatures using analysis of variance.

Experiment 3

Standard metabolic rate of each individual was extrapolated from data collected in experiment 2. Mean standard metabolic rate of the group was compared to the mean dormant (night-time) metabolic rate using t-tests. This analysis was repeated for each

temperature.

Experiment 4

Differences in oxygen consumption of a group of 3 cunner were compared between shelter site treatments using analysis of variance. Within treatments, routine metabolic rates of the group were compared to the average individual routine rate using t-tests. This analysis was repeated for each temperature.

RESULTS

Amplitude and duration of apparent SDA

At 5°C, cunner remained active throughout the day, but would not feed. At 10°C and 15°C, postprandial oxygen consumption rose rapidly to reach a maximum about 2 hr after feeding (Fig. 1.1). For both 10°C and 15°C, the increase in oxygen consumption due to SDA was approximately 100 mg O₂ kg⁻¹ hr⁻¹. This represented an increase over unfed controls (Fig. 1.1) of approximately 1.7 times at 10°C and 1.6 times at 15°C. The difference in amplitude was not statistically significant (t-test, $t = 5.1$, $p > 0.05$). Duration of apparent SDA was significantly longer at 10°C than at 15°C (t-test, $t = 5.3$, $p < 0.05$); oxygen consumption returned to pre-feeding levels by 12 hr at 10°C and by 8 hr at 15°C. The total magnitude of SDA (i.e. the area under the oxygen consumption

Fig. 1.1 Oxygen consumption of fed and unfed 0+ cunner at (a) 10°C and (b) 15°C. Cunner were fed to satiation (200 mg of finely chopped shrimp) at time = 0 hrs. Swimming speed was maintained at 1.5 cm sec⁻¹. Vertical error bars represent ± 1 standard deviation. Standard and active metabolic rates (see Fig. 1.3) are provided as a reference. The SDA elicited by this meal should approximate that caused by a natural diet, which is composed mainly of various small crustacea.

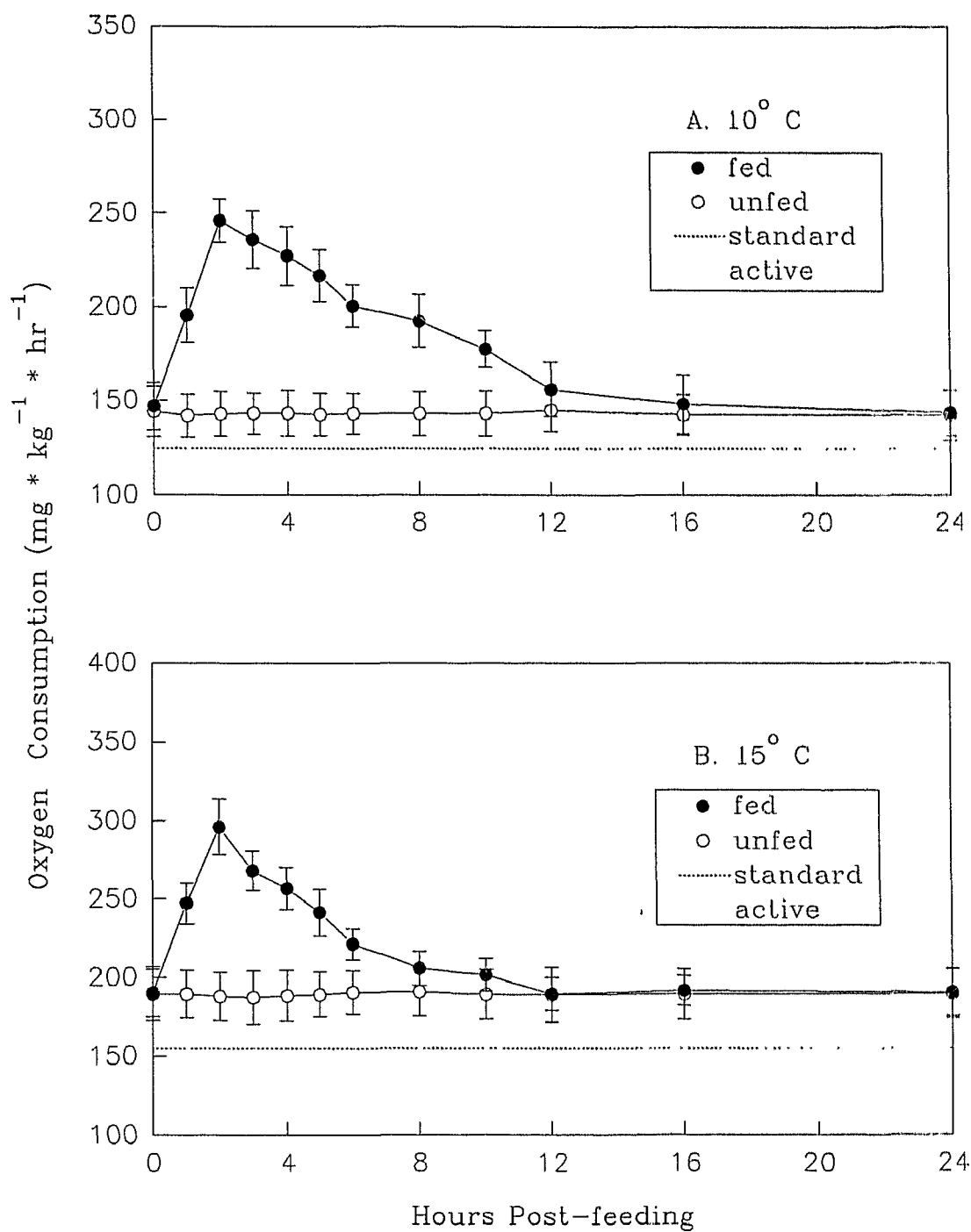


Fig. 1.1

curve in Fig. 1.1) was significantly greater at 10°C ($x = 893 \text{ mg O}_2 \text{ kg}^{-1}$) than at 15°C ($x = 765 \text{ mg O}_2 \text{ kg}^{-1}$) (t-test, $t = 0.4$, $p > 0.05$).

Metabolic costs of feeding and locomotion

Fig. 1.2 illustrates the oxygen consumption of fed and unfed cunner over a range of swimming speeds, based on data pooled from all individuals. As in Experiment 1, cunner would not feed at 5°C. Standard metabolism is represented by the y intercept of the 'unfed' regressions. Swimming regressions for the unfed fish were as follows: (i) at 5°C, $\text{VO}_2 = 93.4 \text{ mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1} + 68.8$ (swimming velocity in body lengths s^{-1}), $r^2 = 0.825$, $p < 0.0001$; (ii) at 10°C, $\text{VO}_2 = 124.4 \text{ mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1} + 63.1$ (swimming velocity in bl s^{-1}), $r^2 = 0.871$, $p < 0.0001$; and (iii) at 15°C, $\text{VO}_2 = 155.1 \text{ mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1} + 51.5$ (swimming velocity in bl s^{-1}). The elevation of the unfed regression line differed significantly between temperatures (t-test between slopes, $t > 6.4$, $p < 0.0001$ for all pairwise comparisons). The slope of the unfed swimming regression did not vary between 5°C and 10°C (t-test, $t = 0.7$, $p > 0.05$), but was significantly lower at 15°C than at 5°C or 10°C. Resting (fed) metabolism (i.e. standard + apparent SDA) for each treatment is shown as the y intercept of the 'fed' regressions. Swimming regressions for the fed fish were as follows: (iv) at 10°C, $\text{VO}_2 = 180.8 \text{ mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1} + 65.1$ (swimming velocity in bl s^{-1}), $r^2 = 0.887$, $p < 0.0001$; and (v) at 15°C, $\text{VO}_2 = 230.3 \text{ mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1} + 44.6$ (swimming velocity in bl s^{-1}). In fed fish, both the slope and the elevation of the swimming regression differed significantly between temperatures (t-test, $t = 6.8$, $p <$

Fig. 1.2 The relationship between oxygen consumption and swimming speed for fed and unfed 0+ cunner at (a) 5°C, (b) 10°C, and (c) 15°C. 'Fed' fish were given 200 mg of finely chopped shrimp. Oxygen consumption was measured for 30 min at 1 cm sec⁻¹ and at 5 cm sec⁻¹ increments from 5 cm sec⁻¹ until the critical swimming speed was attained. The experiment was repeated 3 times on each of 5 individuals.

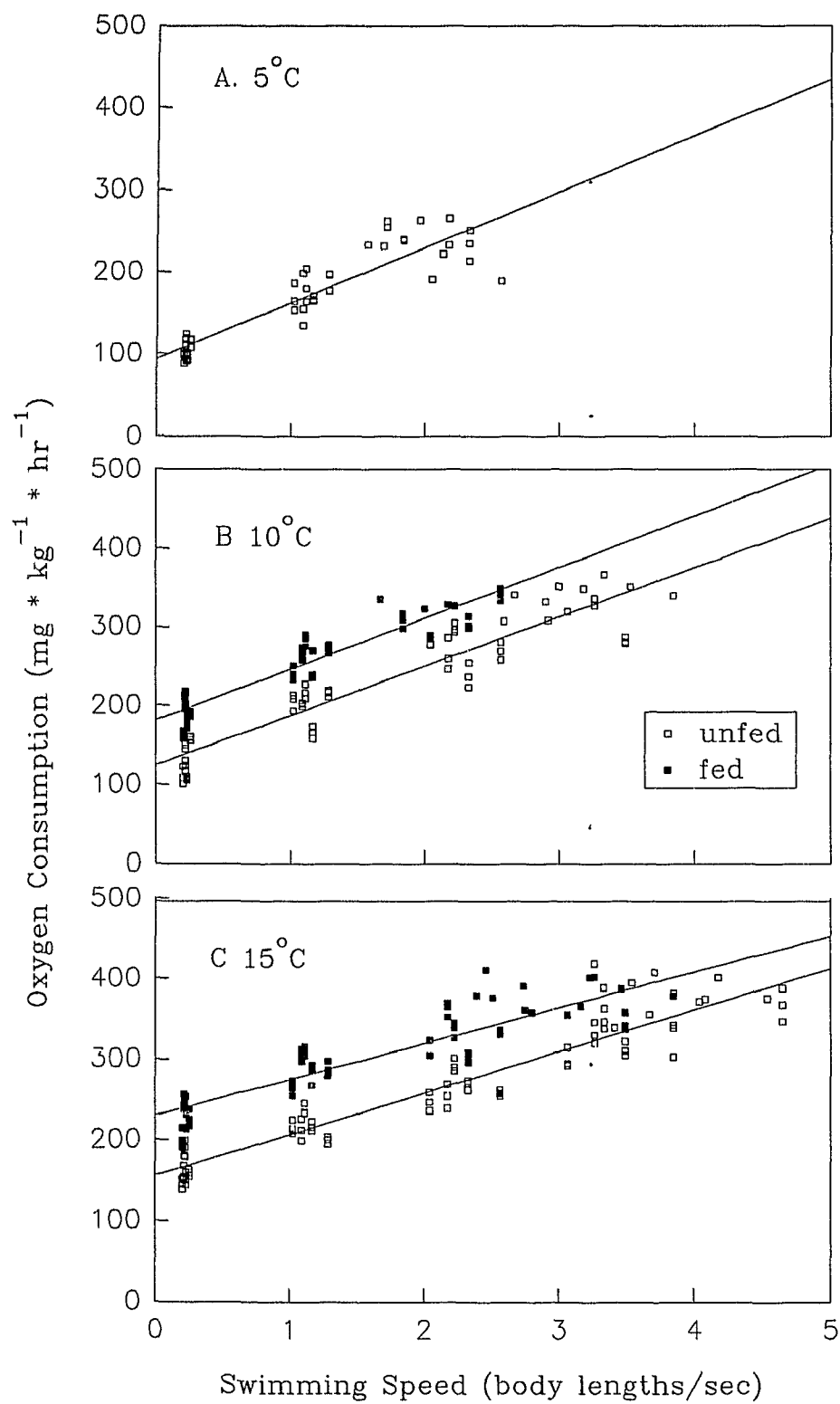


Fig. 1.2

0.001 and $t = 8.2$, $p < 0.0001$, respectively). As in unfed fish, the slope of the regression line was significantly lower at 15°C than at 10°C. The difference in elevation between the unfed and fed regression lines in Figs. 1.2b and 1.2c is the apparent SDA at each swimming speed. Oxygen consumption due to apparent SDA was 56.4 mg O₂ kg⁻¹ hr⁻¹ at 10°C and 75.1 mg O₂ kg⁻¹ hr⁻¹ at 15°C. At both 10°C and 15°C, the increase in oxygen consumption attributed to apparent SDA was statistically significant (t-test, $t = 10.3$ for 10°C, $t = 9.7$ for 15°C, $p < 0.0001$ for both temperatures).

The standard metabolic rate, active metabolic rate, critical swimming speed and scope for activity of cunner were also determined for individuals. Standard metabolism of unfed fish increased significantly with temperature (ANOVA, $F = 23.6$, $p < 0.001$) in a more or less linear fashion (Fig. 1.3). Active metabolism of unfed fish also increased with temperature (ANOVA, $F = 29.4$, $p < 0.001$; Fig. 1.3). The increase in active metabolism was greater from 5°C to 10°C than from 10°C to 15°C. Resting metabolism (i.e. standard + SDA) of fed fish increased significantly from 10°C to 15°C (t-test, $t = 5.6$, $p < 0.05$), as did active metabolism (t-test, $t = 8.2$, $p < 0.01$; Fig. 1.3). Active metabolism did not differ between fed and unfed fish at either 10°C or 15°C (t-test, $t = 0.3$, $p > 0.05$ for both temperatures; Fig. 1.3). Thus the reduction of scope due to apparent SDA occurred from an increase in the resting rate of metabolism, rather than a decrease in the active rate.

Critical swimming speed increased significantly with temperature in both unfed (ANOVA, $F = 137.4$, $p < 0.0001$) and fed (t-test, $t = 7.1$, $p < 0.0001$) cunner (Fig. 1.4). However, at a given temperature, critical swimming speed was much lower in fed fish than in unfed fish (t-test, $t = 6.4$, $p < 0.0001$ for both 10°C and 15°C), indicating that

Fig. 1.3 Mean standard and active metabolic rates of fed and unfed 0+ cunner at three temperatures (5°C, 10°C and 15°C). Means are derived from triplicate runs on each of 5 individuals. Vertical error bars represent ± 1 standard deviation.

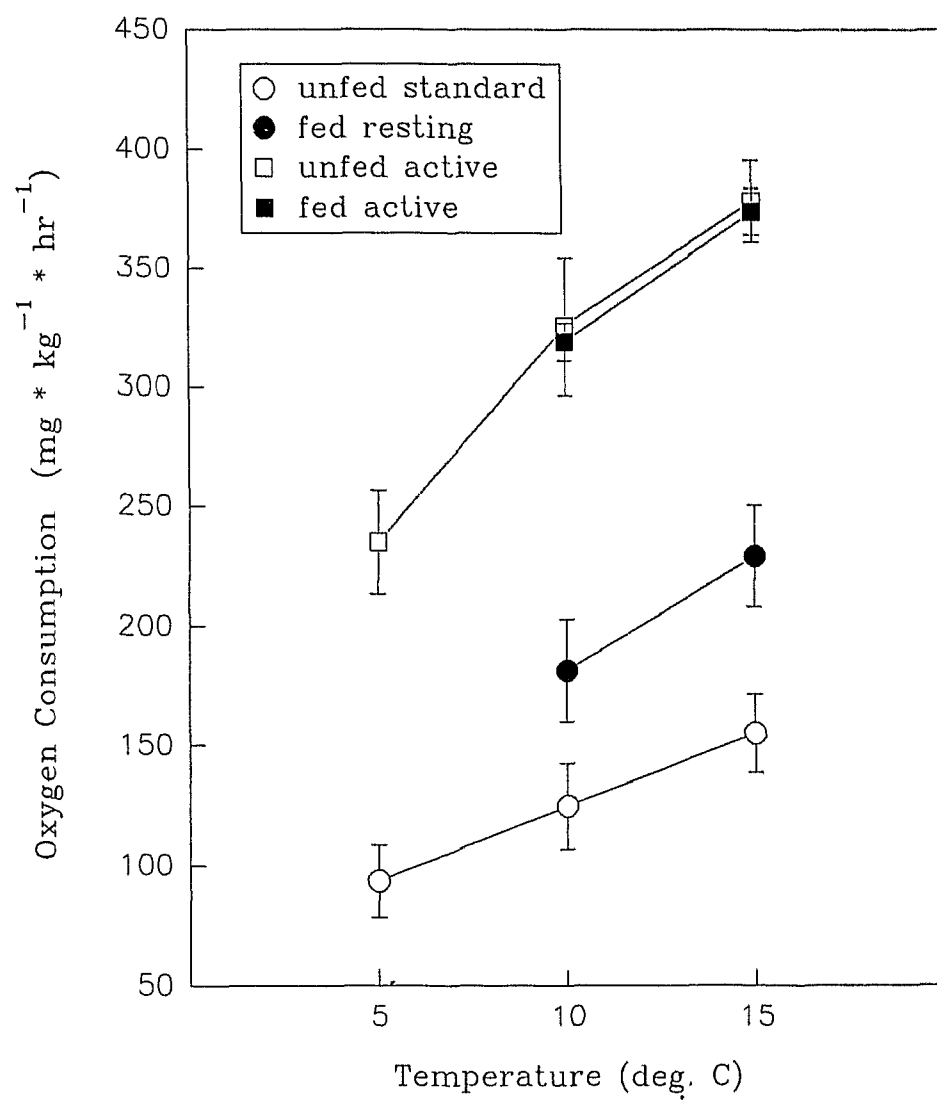


Fig. 1.3

Fig. 1.4 Critical swimming speed (body lengths s^{-1}) of fed and unfed 0+ cunner at three temperatures (5°C, 10°C and 15°C). Means were derived from triplicate runs on each of 5 individuals. Vertical error bars represent ± 1 standard deviation.

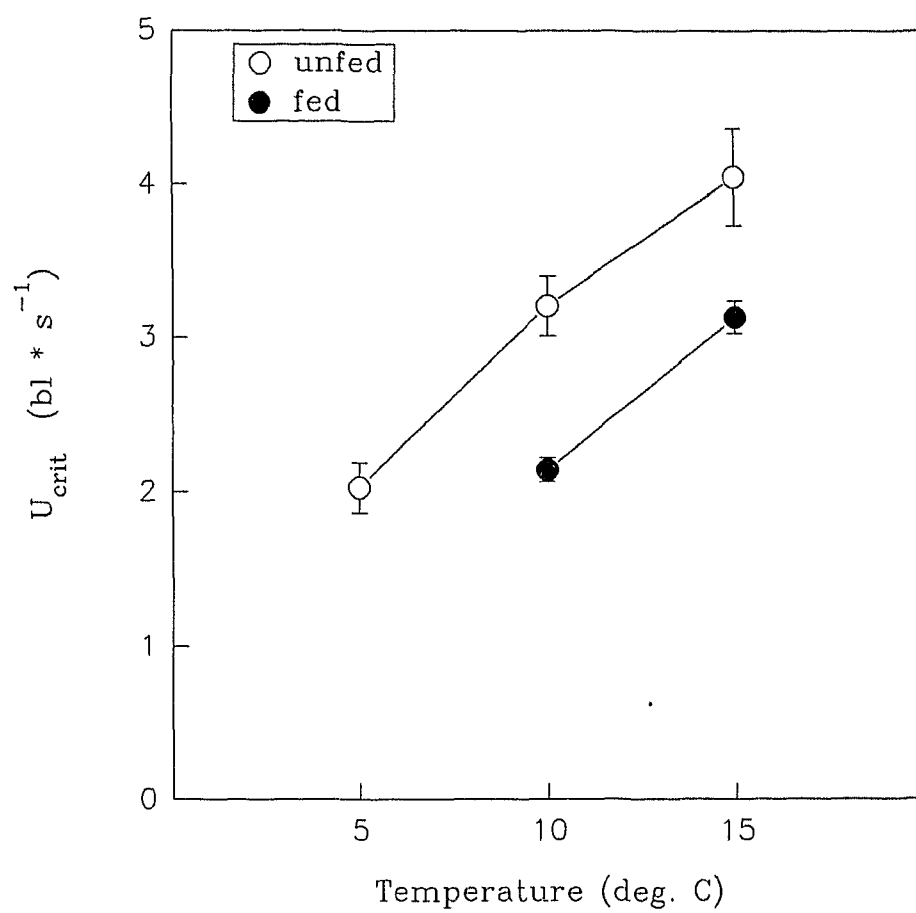


Fig. 1.4

energy was allocated away from locomotion and into feeding and digestion. Scope for activity increased significantly with temperature in unfed fish (ANOVA, $F = 18.9$, $p < 0.001$; Fig. 1.5) but not in fed fish (t -test, $t = 0.4$, $p > 0.05$). At a given temperature, scope for activity was significantly lower in fed fish than in unfed fish (t -test, $t = 7.3$, $p < 0.001$ for 10°C ; $t = 5.9$, $p < 0.001$ for 15°C).

Diel and seasonal variation in standard metabolic rate

Mean oxygen consumption of cunner dormant overnight was compared to mean values of standard metabolism extrapolated from individual swimming regressions in experiment 2 (Fig. 1.6). For all temperature treatments, dormant metabolism was significantly lower than the daytime standard metabolism extrapolated from swimming regressions (t -test, $t \geq 4.4$, $p < 0.05$ for all temperatures). As temperatures increased, the difference between night-time dormant and daytime standard metabolic rates decreased from a 60% reduction at 5°C to a 10% reduction at 15°C . This suggests that cunner enter a 'deeper' state of dormancy as water temperatures decrease.

Metabolic cost of shelter site defense

The number of shelter sites present had a profound effect on the routine oxygen consumption of groups of young-of-the-year cunner. The cumulative routine metabolic rate of a group of 3 fish presented with varying amounts of shelter is shown relative to

Fig. 1.5 Mean scope for activity of fed and unfed 0+ cunner at three temperatures (5°C, 10°C and 15°C). Means were derived from triplicate runs on each of 5 individuals. Vertical error bars represent ± 1 standard deviation.

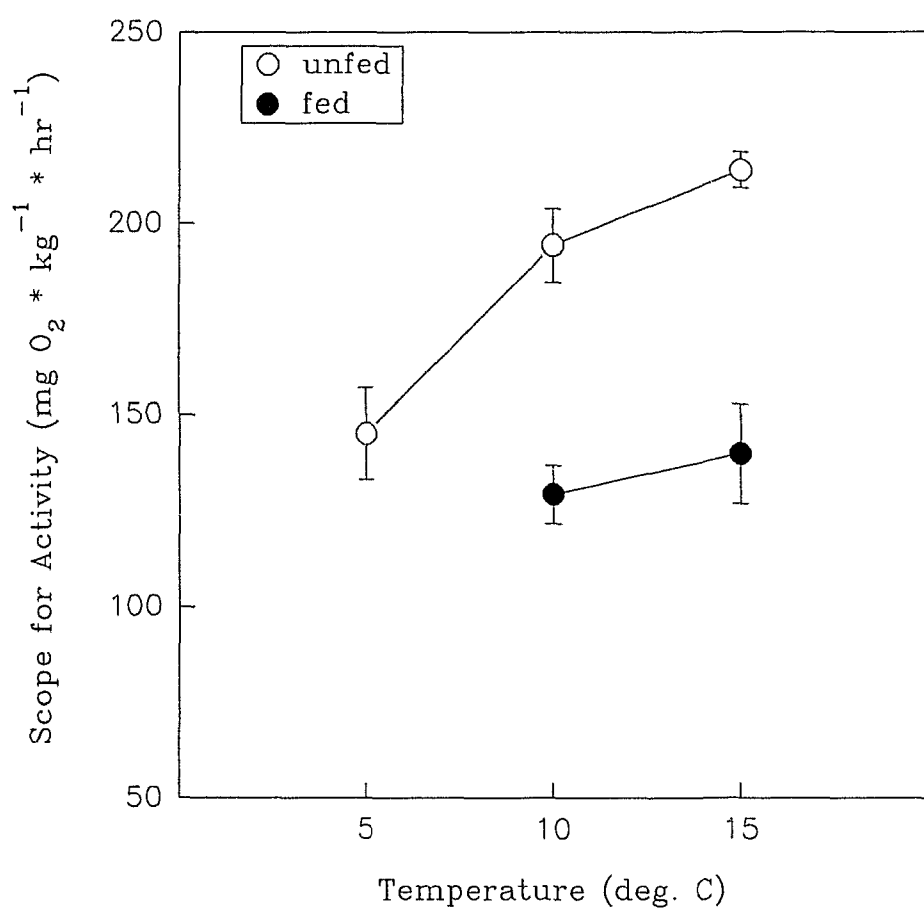


Fig. 1.5

Fig. 1.6 Mean oxygen consumption of unfed 0+ cunner during daytime rest and nocturnal torpor. Means are derived from triplicate runs on each of 5 individuals. Vertical error bars represent ± 1 standard deviation.

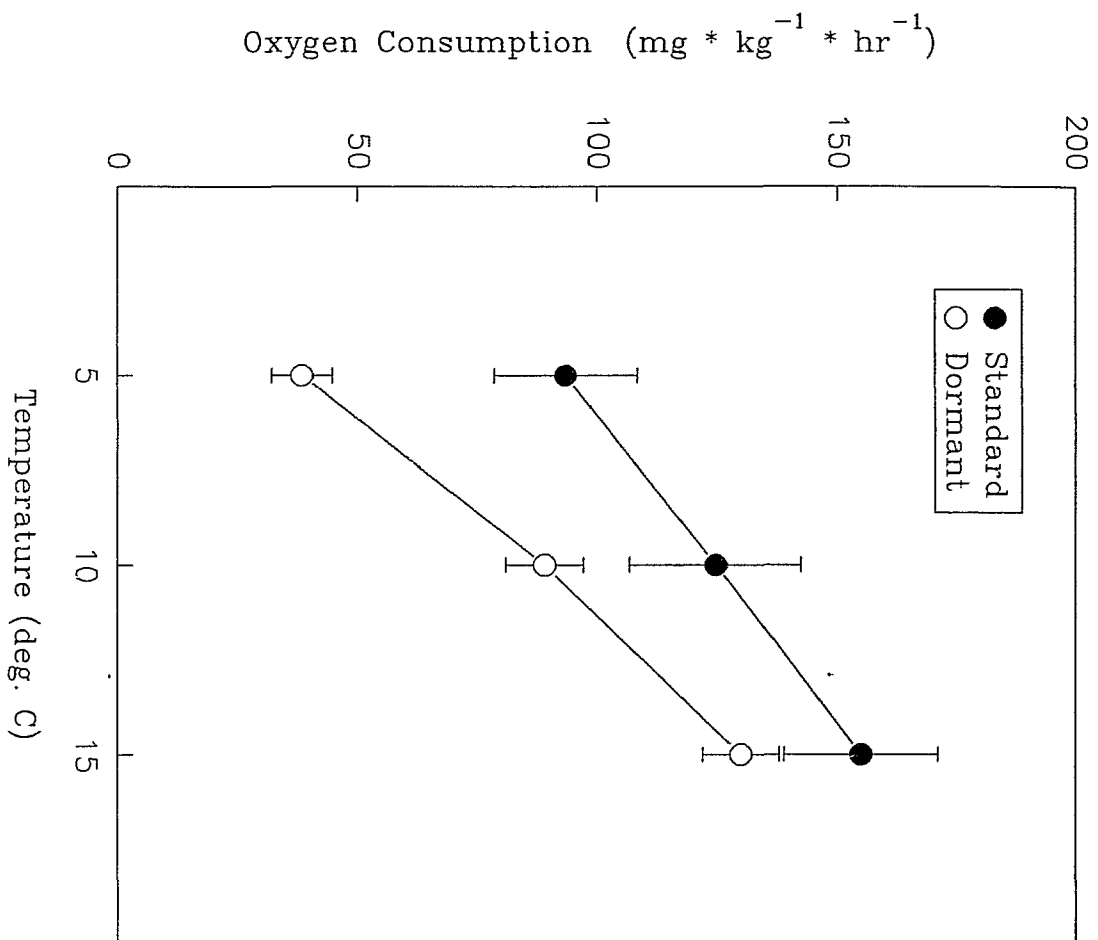


Fig. 1.6

their individual routine and active metabolic rates in Fig. 1.7. The relationship between oxygen consumption and shelter availability was very similar between temperatures; i.e. the rate of oxygen consumption was simply elevated at higher temperatures. Analysis of variance indicated that significant differences in oxygen consumption occurred between treatments (number of shelter sites) ($F = 155.8$, $p < 0.0001$). Post-hoc multiple comparisons (Tukeys' HSD) indicated that treatments could be classified under three groups according to their effects. A complete lack of shelter elicited a torpor response (Auster 1989), in which the 3 individuals huddled closely together and entered the dormant state, irrespective of temperature. The cumulative oxygen consumption of each zero-shelter group was 12-19% lower than the sum of their individual routine rates; this difference was significant at all three temperatures (t-test, $t \geq 4.5$, $p < 0.05$ for all temperature treatments). When 1 or 2 shelter sites were present, a radically different result was obtained. Intense and often violent agonistic interactions occurred between individuals attempting to occupy the same refuge (Fig. 1.8). This resulted in a 200-250% increase in oxygen consumption over the sum of the individual routine rates, to nearly 100% of the cumulative scope for activity (Fig. 1.7). With 3 or 4 shelter sites present, the routine oxygen consumption of the group dropped to a level not significantly different from the sum of the individual rates (t-test, $t \leq 1.2$, $p > 0.05$ for all temperature treatments; Fig. 1.7). Occasional aggression was observed between individuals when 3 or 4 shelter sites were present (Fig. 1.8), but this behaviour did not significantly affect the routine metabolic rate of the group. Thus, three types of effects were demonstrated: a decrease in routine metabolic rate in the absence of any shelter, a dramatic increase in

Fig. 1.7 Oxygen consumption of groups of 3 unfed 0+ cunner presented with a range of shelter site availability. Data are presented relative to the active and standard metabolic rates of the group. Individual routine = routine metabolic rate of individual cunner. Group routine = routine metabolic rate of a group of 3 cunner sharing the chamber. Active = active metabolic rate of cunner from Fig. 1.3. The experiment was conducted at (a) 5°C, (b) 10°C, and (c) 15°C. Vertical error bars represent ± 1 standard deviation.

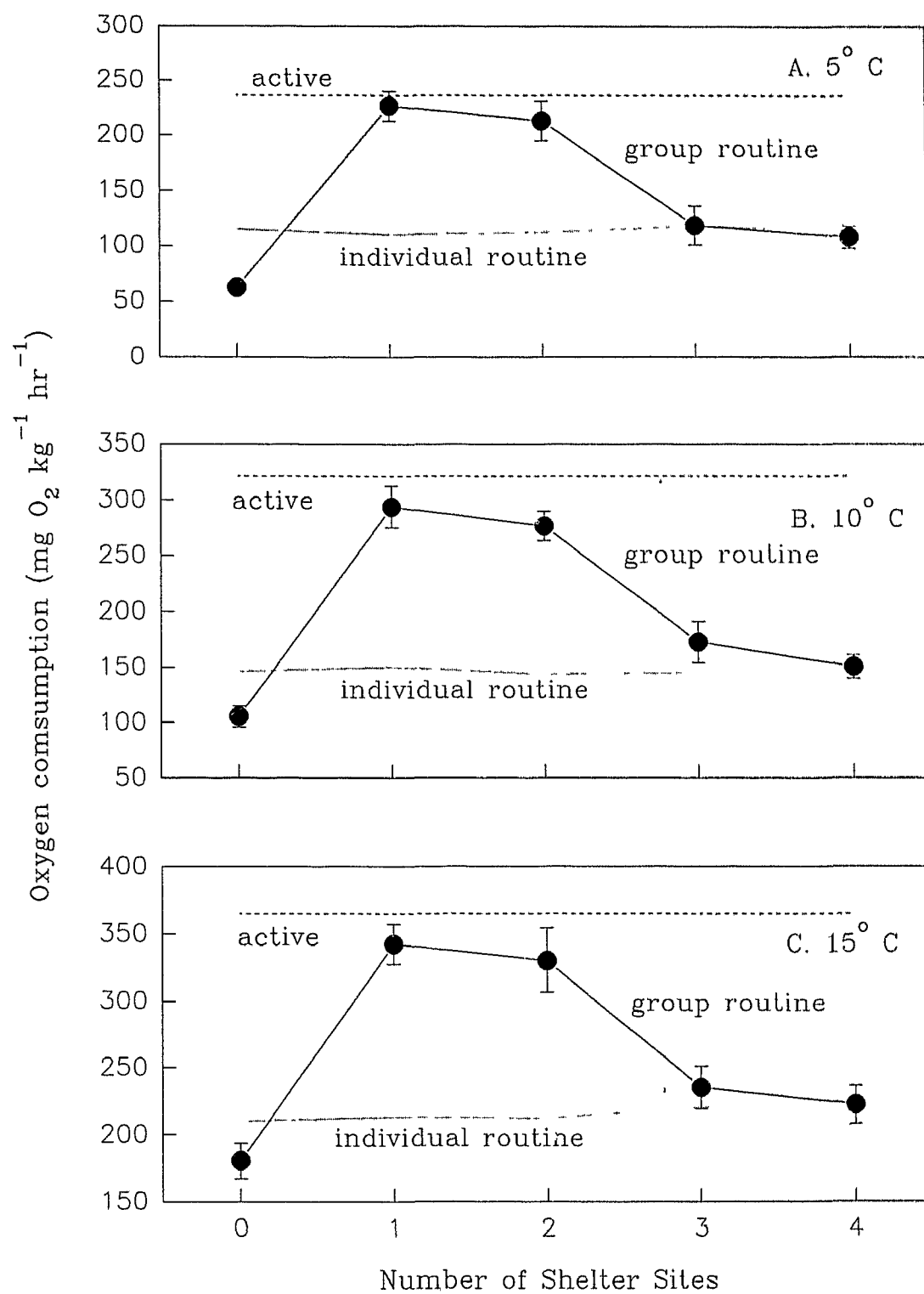


Fig. 1.7

Fig. 1.8 The number of agonistic interactions (bites min⁻¹) between unfed 0+ cunner presented with a range of shelter site availability. The experiment was conducted at 5°C, 10°C and 15°C. Vertical error bars represent ± 1 standard deviation.

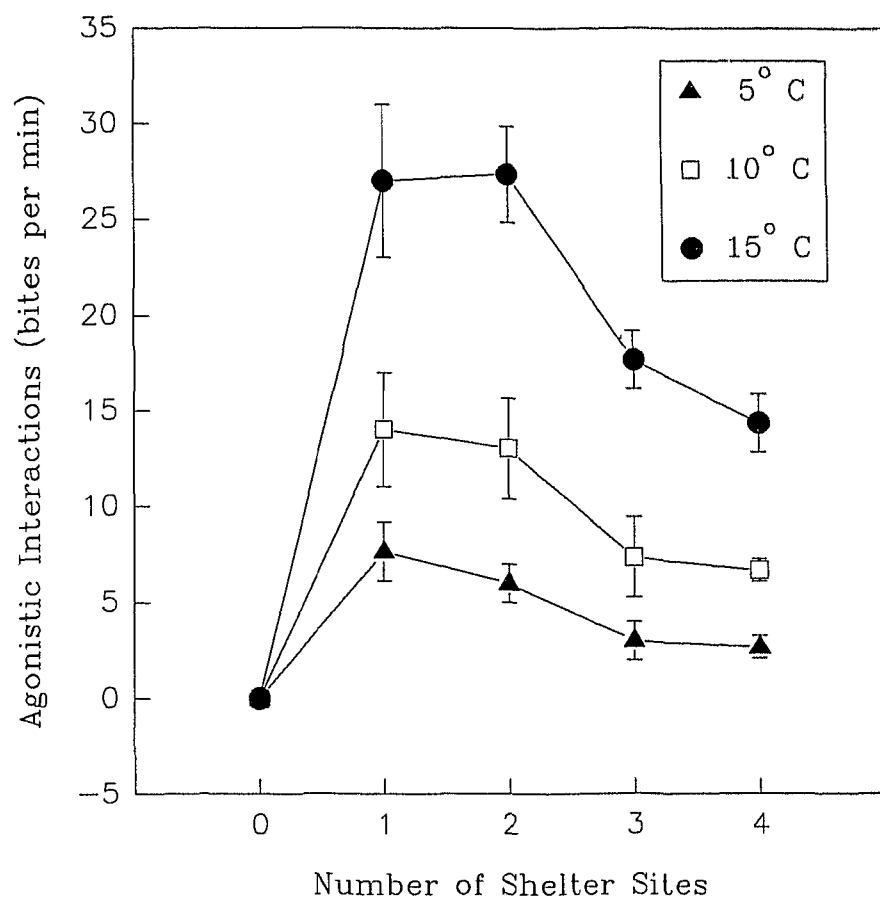


Fig. 1.8

routine metabolic rate when shelter is present but inadequate, and no change in routine metabolic rate when shelter is in adequate supply.

DISCUSSION

Apparent Specific Dynamic Action

The peak amplitude of apparent SDA in cunner fed to satiation was 1.6-1.7 times the standard metabolic rate (Fig. 1.1). Jobling (1981) reported that peak amplitude of apparent SDA in several species of fish ranged from 1.5-2.5 times the 'resting' (i.e. standard or low routine) rate, although activity was not always accounted for in the studies he cited. Thus, amplitude of apparent SDA in cunner appears to fall within the lower range of published values for fish. However, duration of SDA in cunner is much lower than previously reported for other fish species. In this study, oxygen consumption of fed cunner returned to pre-feeding levels within 12 hr at 10°C and within 8 hr at 15°C (Fig. 1.1). In contrast, the duration of SDA ranges from 25 hr at 20°C to 55 hr at 10°C in plaice (Pleuronectes platessa; Jobling 1980), 30 hr at 20°C in largemouth bass (Micropterus salmoides; Beamish 1974), 50 hr at 23°C in aholehole (Kuhlia sandvicensis; Muir and Niimi 1972), and 100 hr at 8.5°C in sablefish (Anpllopoma fimbria) (Furnell 1986). Duration of SDA in the temperate blenny, Blennius pholis, is more like that of cunner (20 hr at 10°C; Vahl and Davenport 1979). Of all fish species in which SDA has been studied, B. pholis is perhaps the most ecologically similar to

cunner; both species inhabit shallow nearshore waters of the temperate north Atlantic Ocean and have similar dietary requirements. The short duration of SDA in conner may in part be due to their simplified digestive system, which lacks a stomach (Chao 1972). Conner have strong, tusk-like teeth which are used to masticate their prey, which then passes through the esophagus and into the straight-tube intestine. Pepsins are secreted by the intestine, which is the major site of proteolysis (Chao 1972). While intestinal evacuation rates have not been determined for this species, they are likely to be quite high, due to the simplicity of the digestive system. Thus, the observed pattern of a rapid onset and short duration of apparent SDA may be explained by the peculiar digestive system of conner.

The proportion of scope for activity taken up by apparent SDA ranges from 30-50% in most fish species studied, although Soofiani and Hawkins (1982) reported that SDA in juvenile North Sea cod (Gadus morhua) could rise to 98% of the aerobic scope. In experiment 1 of this study, the peak amplitude of apparent SDA reduced the scope for activity of conner by 57% at 10°C and by 53% at 15°C (Fig. 1.1). In experiment 2, the mean reduction in scope due to feeding was 29% at 10°C and 35% at 15°C (Fig. 1.5). In summary, conner fed to satiation retain about one half to two thirds of their scope for activity. This value is in general agreement with studies of SDA in other fish species.

Allocation of energy to feeding and locomotion

Furnell (1986) measured the oxygen uptake of fed and unfed sablefish (Anoplopoma

fimbria) over a range of swimming speeds. He found that the swimming regressions of fed and unfed fish intersected, i.e. as swimming speed increased, the energy allocated to digestion decreased, until the cost of swimming equalled the scope for activity. In cunner, the slopes of the fed and unfed swimming regressions did not differ at 10°C or at 15°C, indicating that apparent SDA was constant over the entire range of swimming speeds. Instead, at higher swimming speeds energy was allocated away from locomotion, resulting in a reduction of the critical swimming speed with no concomitant reduction in active metabolic rate (Fig. 1.2). Differences between cunner and sablefish may reflect differences in how the blood supply is distributed during exercise between the locomotory muscle and the digestive tract (Randall and Daxboeck 1982).

Furnell (1986) suggested that adult sablefish (Anoplopoma fimbria) allocate energy to locomotion rather than digestion in order to maximize their prey capture ability. Adult sablefish are large, midwater pelagic predators and are continuously active (Furnell 1986). Age 0+ cunner are relatively sedentary carnivores that suction feed on small benthic organisms, mainly in the morning and late afternoon (Levin 1994b; Chapter 2). Their small size renders them vulnerable to predation (Chapter 4), therefore their need for rapid growth outweighs their need for sustained locomotion. Beamish (1974) found that energy expenditure in the largemouth bass (Micropterus salmoides), a relatively sedentary ambush predator, was also preferentially allocated to digestion rather than locomotion. The physiological mechanism responsible for allocation of energy among multiple metabolic demands is poorly understood in fish (Furnell 1986). Randall and Daxboeck (1982) have suggested shunting of blood between the liver, stomach, and body musculature as the

most likely mechanism for diversion of oxygen to the necessary tissues.

Effects of temperature on feeding and locomotory metabolism

In cunner, as with most species, an increase in temperature will lead to a decrease in the duration of apparent SDA, as rates of metabolism and gastric evacuation increase (Jobling 1981). Peak amplitude of apparent SDA for a given ration does not appear to be greatly influenced by temperature (this study), although fish in their natural environment may eat larger rations as temperatures increase and thus raise their peak SDA (Jobling 1981). However, the magnitude of SDA decreases with increasing temperature (Brett and Groves 1979; Jobling 1981; this study); thus food conversion appears to be more efficient at higher temperatures. This may result in faster growth of cunner at higher temperatures (see Chapter 5, Fig. 5.2). In St. Margaret's Bay, cunner settle from the plankton in late August and September, when water temperatures are warmest and growth rates are highest (see Chapter 5, Fig. 5.1). This strategy may be advantageous to 0+ cunner in that it ensures a minimum of time spent in the smallest size classes, which are considered most vulnerable to predation (Post and Evans 1989; Juanes 1994).

Swimming capacity and scope for activity are also dependent on temperature; both tend to increase with temperature to a maximum and thereafter decrease (Beamish 1978; Brett and Groves 1979). The effect of temperature on swimming performance can be profound. The critical swimming speed of age 0+ (22 mm) smallmouth bass (Micropterus

dolomieu) increased from 4.8 to 31.2 cm s⁻¹ (2.2 to 14.2 bl s⁻¹) between 5°C and 30°C, then decreased to 28 cm s⁻¹ (12.7 bl s⁻¹) at 35°C (Larimore and Duever 1968). The critical swimming speed of young (20 cm) sockeye salmon (Onchorhynchus nerka) increased from 50 cm s⁻¹ (2.5 bl s⁻¹) at 1°C to 90 cm s⁻¹ (4.5 bl s⁻¹) at 15°C and thereafter decreased to 80 cm s⁻¹ at 25°C (Brett 1964). In the present study, critical swimming speed of age 0+ (39-46 mm) cunner varied from 2.0 bl s⁻¹ at 5°C to 4.0 bl s⁻¹ at 15°C (Fig. 1.4). In general, maximum critical swimming speed of eurythermal temperate species occurs at 25-30°C (Brett and Groves 1979). Although cunner are known to tolerate waters of 26°C within the southern limits of their range, cunner in St. Margarets Bay rarely encounter temperatures above 18°C, and the effects of higher temperatures on northern populations of this species are unknown.

Nocturnal and overwinter torpor

Many species of diurnally active demersal fish are known to exhibit a night-time quiescent or sleep phase, usually spent within a shelter site (Helfman 1976). However, few species of fish are known to remain dormant throughout winter. Cunner and a closely related species, the tautog (Tautoga onitis) exhibit nightly dormancy at temperatures of 6-7°C and above (Auster 1989). Below 6-7°C, cunner and tautog exhibit overwinter dormancy ('hibernation'). Few studies have been conducted to determine the effects of these behaviours on the metabolic rate of fishes. However, both hibernation and spontaneous nightly torpor are well studied in small mammals, in which thermal

regulation during winter is an energetically expensive proposition at a time when food is usually scarce (Heldmaier 1989). The ability to depress oxygen consumption below the standard metabolic rate can confer considerable energy savings during periods of low temperatures and/or insufficient food supply. Small hibernating mammals such as marmots and ground squirrels can reduce their standard metabolic rates to more than 90% below the standard rate at normothermia (Heldmaier 1989). Despite periodic arousals, this may result in an energy savings of 82-96% over individuals that remain active throughout winter (Geiser 1988). In the present study, the metabolic rate of dormant cunner at 5°C was nearly 60% lower than the standard metabolic rate at that temperature (Fig. 1.6). Other species of small mammals, including bats, mice and hamsters, show spontaneous daily (or nightly) torpor in which the standard metabolic rate can be reduced by greater than 50%, resulting in a total energy savings of 5-50% of the average daily expenditure (Heldmaier 1989). Nocturnal torpor in cunner reduced the standard metabolic rate by about 10% at 15°C and about 25% at 10°C. Thus, cunner appear to rely more heavily on torpor as an energy-saving process at low temperatures during the winter months, when food may be less plentiful in shallow nearshore habitats. However, nocturnal torpor could also be useful during the warmer months as a buffer against 'energy deficits' created by the combined metabolic loads of feeding, locomotion and shelter site defense, or by lack of food.

Energetics of competition

To date there are no published studies directly addressing the energetics of competition between individual fish or fish species. Opportunistic measurements of oxygen uptake during periods of intraspecific aggression have been made for both pumpkinseed sunfish (Lepomis gibbosus) and sockeye salmon (Oncorhynchus nerka). In both cases, the energetic cost of the aggressive interactions was about 50% of the scope for activity (Brett and Groves 1979). In contrast, the metabolic cost of shelter site defense in cunner reached 90-95% of the scope for activity. Population size of juvenile cunner can be limited by availability of shelter (Levin 1991, 1993) and shelter is particularly important during the night-time torpid state. It appears that cunner will expend a great deal of energy in order to acquire a shelter site. Interestingly, a complete lack of shelter elicited a stress response (Auster 1989) in which individual cunner huddled together and entered the torpid state. The significance of this behaviour is unclear, although it is likely to involve conservation of energy and a reduction in the risk of predation.

Conclusions: energy budget

As demonstrated by Priede (1985) for cod (Gadus morhua) and brown trout (Salmo trutta), the maximum values of each component of the energy budget of cunner (standard metabolism, locomotion, SDA and shelter site defense) add up to a sum much higher than

the active metabolic rate. Cunner must therefore allocate energy to each component so that the scope for activity is not exceeded. The pattern of allocation should serve to maximize the animals' growth and survival. For example, energy expenditure in fed fish is directed to feeding and growth and away from sustained locomotion. The high mortality of early juvenile fishes is generally ascribed to size-selective predation concentrating on smaller size classes (Post and Evans 1989; Juanes 1994), so fast growth may be necessary to minimize the effects of predation pressure. While higher swimming speeds may enable juvenile fish to escape predators, this is more likely a function of anaerobically powered burst-swimming than sustained aerobic swimming (Beamish 1978).

Competition for shelter sites is an important component of the energy budget of cunner and can account for almost the entire scope for activity when shelter is limiting. Food can also be limiting at high population densities (Jones 1987a, Forrester 1990). If energy (i.e. food) uptake cannot meet the multiple demands of maintenance, foraging, growth and shelter site defense, then an energy deficit may result, which may be buffered by periods of torpor.

Temperature affects all components of the energy budget and therefore affects the allocation of energy among those components. Swimming capacity and scope for activity are greatly reduced at low temperatures. Thus, large investments of energy into foraging and shelter site defense are not possible at low temperatures. This may partially explain the existence of the overwintering hibernation strategy in cunner.

CHAPTER 2

TIME AND ENERGY BUDGETS OF THE TEMPERATE REEF FISH

(TAUTOGOLABRUS ADSPERSUS)

INTRODUCTION

The allocation of time and energy among activities necessary for self-maintenance, growth and reproduction, is of great importance to the ecology of any animal (Wolf and Hainsworth 1971; Wootton 1990). Animals must allocate these limited resources in a fashion that favours their genetic representation in future generations (Sibly and Calow 1986). To accomplish this, animals must develop and maintain a somatic body which is responsible for transforming energy into offspring (Pianka 1976). This imposes a cost in terms of the energy allocated to growth and the time spent on foraging to provide that energy. Time and energy may be required for other activities such as reproduction, shelter site defense, and predator avoidance (Schartz and Zimmerman 1971; Stiles 1971; Wolf and Hainsworth 1971; Hertz et al. 1988; Hixon and Carpenter 1988; Goldstein 1988; Reichart 1988).

In fish, the allocation of time and energy takes place in a spatio-temporally variable

environment (Wootton 1990). Abiotic factors, such as temperature, and biotic factors such as predation risk or competitor density may influence patterns of allocation. Wootton (1990, p.5) suggested that a central problem in ecology "is to determine the responses that individuals make in terms of their allocation of time and energy in the face of environmental variability. The allocation patterns, through their effects on survival and reproduction, will determine the lifetime reproductive success of individuals, that is their fitness".

Studies of time and energy budgets require that the relative effort spent on various activities be quantified, requiring the construction of time budgets to which the appropriate metabolic costs, generally measured by some form of respirometry, are then applied (Wolf and Hainsworth 1971). This type of study has rarely been attempted with fish, probably due to the difficulty in observing fish in their natural habitat over sufficiently long periods of time. Most studies of time and energy budgets have been performed on reptiles (Hertz et al. 1988) and birds (Verbeek 1964; Schartz and Zimmerman 1971; Goldstein 1988), particularly territorial hummingbirds (Pearson 1954; Stiles 1971; Wolf and Hainsworth 1971; Hixon and Carpenter 1988) whose limited territory size allows them to be observed for a complete diurnal activity period.

Daily time budgets of territorial birds and fishes are generally divided into three major components:

$$T_{\text{tot}} = T_r + T_f + T_d$$

(Wolf and Hainsworth 1971; Hixon 1980; Wootton 1990) where T_{tot} for a daily period would be 24 hr (Wootton 1990), T_r is the time spent resting, T_f is the time spent foraging

and T_d is the time spent defending the territory. In the case of fish, the territory may centre around any defensible resource, such as food, shelter, mates, or offspring. However, in first-year juvenile fish, the primary object of territorial defense is likely to be shelter, as their small size makes them particularly vulnerable to predation (Juanes 1994). The energetic equivalents of the time budget components can be estimated as:

$$E_{tot} = E_r T_r + E_f T_f + E_d T_d$$

where E_{tot} is the total energy expenditure over a 24 hr period, and E_r , E_f and E_d are the metabolic costs per unit time of resting, foraging and territorial (shelter site) defense.

The time (and energy) spent performing an activity will have associated benefits and costs (Hixon 1980; Wootton 1990). For example, the time spent feeding yields a benefit in terms of energy gain and growth, but the costs may include an increased risk of predation, the energetic costs of foraging and digestion, and a decrease in the time and energy available for reproduction (Wootton 1990). An individual should allocate its time and energy in such a way as to maximize the net benefit, i.e. the difference between benefit and cost (Krebs and McCleery 1984). As environmental conditions change (e.g. changes in habitat type, temperature, or light intensity), the net benefit of a given activity may change accordingly (Krebs and Davies 1984). An individual may then be able to maximize its net benefit by changing the allocation of time among various activities. For example, the ability of a juvenile fish to forage and avoid predators may vary with the daily cycle of light and dark (Wootton 1990). Species are usually active only during limited periods within the diel cycle; many juvenile fishes are only active during the daylight hours (Helfman 1993). In addition, the relative costs and benefits of different

activities may change with ontogeny. As juvenile fish grow larger, time spent foraging may become more beneficial than time spent in shelter, since larger fish are generally at less risk of predation (Juanes 1994).

The objective of this chapter is to construct a time budget based on in situ observations of behavioural activities of young-of-the-year cunner (Tautoglabrus adspersus), a temperate reef-dwelling labrid. Young-of-the-year fish are used with the assumption that the lack of reproductive behaviour will simplify the time and energy budgets somewhat. In addition, early juvenile stages are well recognized for their importance to the overall recruitment success of fish species (Jones 1991; de Lafontaine et al. 1992). Energetic costs per unit time of resting in shelter, foraging (including swimming + apparent SDA) and territorial defense were determined for cunner in Chapter 1: these values will be applied to the time budget in order to construct an energy budget for this species. Time and energy budgets will be compared for cunner at different temperatures and for fish of varying size/age, as well as for cunner in different habitats and at different levels of conspecific density.

METHODS

Effects of temperature and size/age

The influence of temperature and size/age on activity were investigated in rocky reef habitats. Newly settled cunner were injected with specific patterns of dots and colours

of acrylic dye, allowing individual fish to be recognized. The waters of St. Margarets Bay are characteristically clear, with average lateral visibility about 10 m (personal observations). This allowed for relatively easy observation of individual cunner for prolonged periods. Study sites were chosen in shallow (< 2 m) water close to shore and observations were made while snorkelling. This provided several advantages over the use of SCUBA, which would limit the observation time to the length of the air supply and would produce bubbles which might disturb the fish.

Time budgets were constructed by observing individual cunner for 2 hr periods. All observations were taken from 1200 to 1400 hr to avoid any possible effects of light intensity and/or circadian rhythms on activity. All activities were timed to the nearest 30 seconds and recorded immediately in a waterproof notebook. A total of ten observation periods (20 hr total) were recorded in each habitat in August and September of 1992. The timed observations were then divided into three categories:

1) Resting: The time the fish spent resting within the shelter site. It was assumed that the fish did not become dormant (i.e. maintained the standard metabolic rate) during the daylight hours (see Chapter 1), but was torpid within 1 hr after sunset (Olla et al 1975).

2) Foraging: The total time spent on prey search and feeding.

3) Defense: The total time spent on agonistic interactions involving defense of a shelter site or food supply, including all swimming involved.

Newly settled cunner are very site-attached (Olla et al. 1975; Chapters 3, 4) and the time spent swimming apart from foraging and defense was negligible. Two-hour observations were also made biweekly from September 1 to December 15, 1991, on 4

reefs. This allowed activity of cunner to be quantified over the first 15 weeks post-settlement, representing a range in size of approximately 10 mm total length (TL) at settlement to 50 mm TL in mid-December, and a range of water temperatures from 18°C on September 1 to 5°C on December 15, 1991. The mean time spent on each activity was calculated and compared between observation dates using a repeated measures analysis of variance, with observation date as a blocking factor and reef as a fixed effect (Sokal and Rohlf 1981).

In addition to quantifying the amount of time spent on each activity, the effect of temperature and size/age on swimming speed was also measured. Since over 90% of all swimming occurred during foraging bouts (personal observations), swimming speed was measured as a means of more accurately determining foraging costs. A 5 m x 5 m polypropylene rope grid of 5 cm squares was placed on the reef surface. The grid was left for 48 hr to allow the fish to become accustomed to it. Swimming speed was measured by counting the number of squares crossed during a timed swimming bout. While this method does not account for swimming in the vertical plane, cunner tended to stay very close to the substrate, minimizing the distance swum vertically (personal observations). As with observations of behavioural activities, all measurements of swimming speed were conducted from 1200 to 1400 hours. At each observation date, cunner of a range of sizes ($n = 11$; approximately 25-60 mm TL, i.e. age 0+ and 1+ fish) were observed. This reduced the possibility of temperature and size being confounded with regards to their effects on swimming speed, although the mean size still tended to increase with time.

Effects of habitat and conspecific density

Behavioural observations of 0+ cunner were made in each of 4 habitat types (rocky reef, cobble bottom, seagrass (*Zostera*) beds, and sandy bottom) in St. Margarets Bay, Nova Scotia during August and September of 1992. Data were used to construct time budgets of activity as above. The mean time spent in each of the three categories (resting, foraging and defense) from the ten observation periods were compared between habitat types using analysis of variance.

The effects of conspecific density were quantified in rocky reef habitat only. Twelve large boulders (glacial erratics), of similar size and at similar depth, and isolated from the nearest neighbouring hard bottom by at least 10 m (see Chapter 3), were used as study reefs. The reefs were randomly divided into three groups of four, designated as low density, control and high density. On low density reefs, density of 1+ and older resident cunner was artificially lowered to 1 individual m^{-2} by removal of individuals using anaesthetic (10% solution of quinaldine sulfate (Sigma) in seawater). Individuals removed from the low density reefs were released at a site on the far side of St. Margarets Bay, about 3 km distant. On control reefs, natural resident density (2.4-3.2 individuals m^{-2}) was not manipulated. On high density reefs, the density of 1+ and older cunner was artificially increased by transplanting cunner from the far side of the bay. Density for this treatment was maintained at 5 individuals m^{-2} . Time budgets were constructed as above, and the mean time allocated to each category was compared between density treatments using analysis of variance.

Diel patterns of activity

In order to determine the total energy expenditure over a 24 hr period, behavioural observations of 5 0+ cunner (20-25 mm total length) were made for the entire daylight period. As it was not possible for an observer to remain in the water for several hours at a time, a series of 1 hr observations was made on consecutive days, each observation period starting 1 hr later than the start of the previous period. For the sake of simplicity, all observations were made within one week of the autumnal equinox (September 21, 1992) to ensure an equal distribution of light and dark within the diel cycle. It was assumed that cunner remained torpid during the hours of dark (Olla et al. 1975).

When data had been gathered for all 5 individuals throughout the entire daylight period, the mean time allocated to each activity was calculated for each hour of the daylight period (i.e. approximately 0600 to 1800 hrs). Time budgets thus constructed allowed for measurement of diel and diurnal changes in allocation of time and energy.

RESULTS

Effects of temperature and size on time budgets

The effects of temperature and size/age on cunner are interactive. Cunner settled to the study sites in early September, when water temperatures were highest (see Chapter 5). As the age and size of cunner increased, water temperature decreased. The temporal

change in time budgets from September 1 to December 15, 1991, is shown in Fig. 2.1. When cunner are newly settled, they spend a large proportion of their time in shelter. As juvenile cunner grow, they spend less time in shelter and more time foraging. However, as water temperature dropped below about 10°C, cunner became less active and began to spend more time resting in shelter and less time foraging. At 5°C, cunner spent > 90% of their time in shelter, with the remaining 10% devoted to shelter site defense. The time allocated to shelter site defense did not appear to be greatly influenced by temperature or size/age, nor did it appear to be related to the proportion of time spent in the shelter.

Swimming speeds of foraging cunner in relation to total length and to temperature are presented in Fig. 2.2. Temperature appears to exert a greater influence on foraging activity than does total length: there is a strong negative relationship between temperature and swimming speed, but no obvious relationship between total length and foraging speed. Interestingly, swimming speed appeared to decrease with temperature in a stepwise fashion, in which 'plateaus' where little change in swimming speed occurred over a range of 2-3°C alternated with sharp decreases in swimming speed over a similar range of temperature (Fig. 2.2).

Effects of temperature and size on energy budgets

Energy budgets of 0+ cunner are shown for temperatures of 5°C, 10°C, and 15°C in Table 2.1; these were the temperatures at which respirometric measures of the costs of various activities were performed in Chapter 1. Since it was not possible to measure the

i

Fig. 2.1 Temporal change in activity budgets (allocation of time to daily activities) of C+ cunner from September 1 to December 15, 1991. The mean proportion of time (± 1 standard error) allocated to each activity was calculated from successive 2 hr observation periods. Data are plotted as a function of date and total length. Water temperature is also presented as a function of date.

t

Fig. 2.1

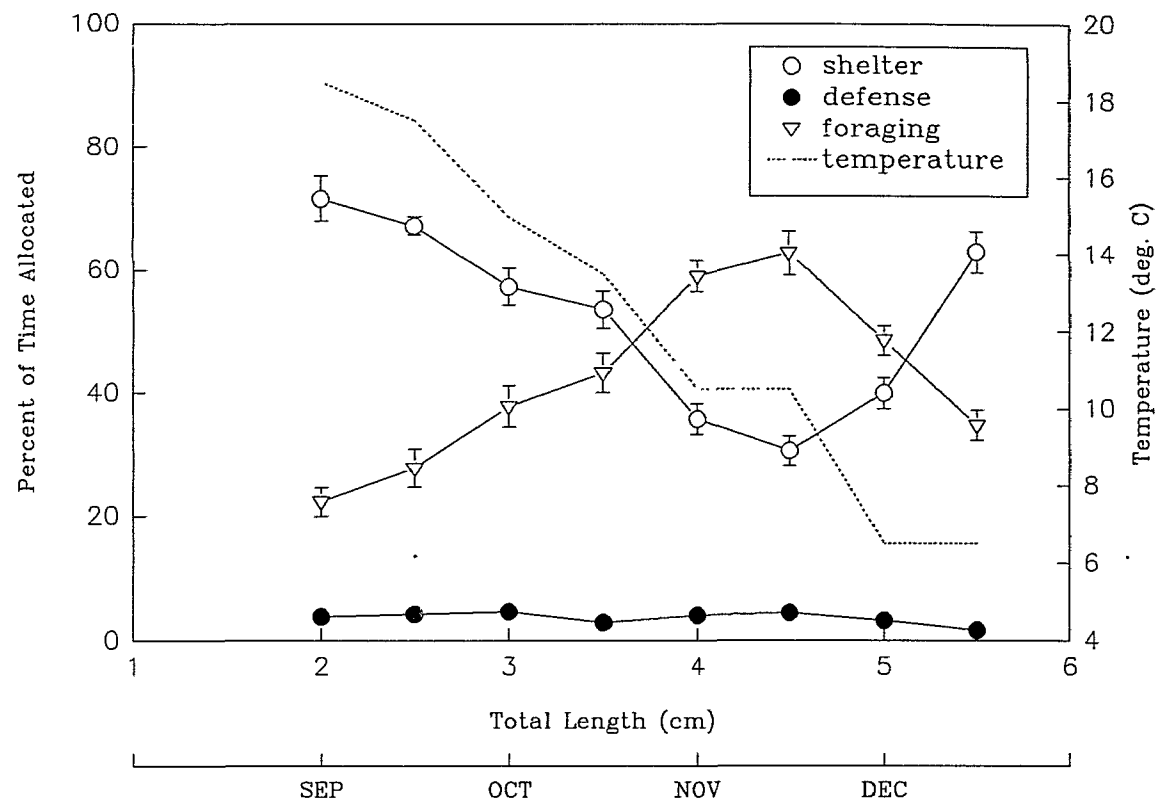


Fig. 2.2 Three-dimensional plot of foraging speed (cm sec^{-1}) of 0+ cunner as a function of temperature and total length. Foraging speed was measured *in situ* by placing a rope grid over the substrate and counting the number of squares over which a fish swam per unit time.

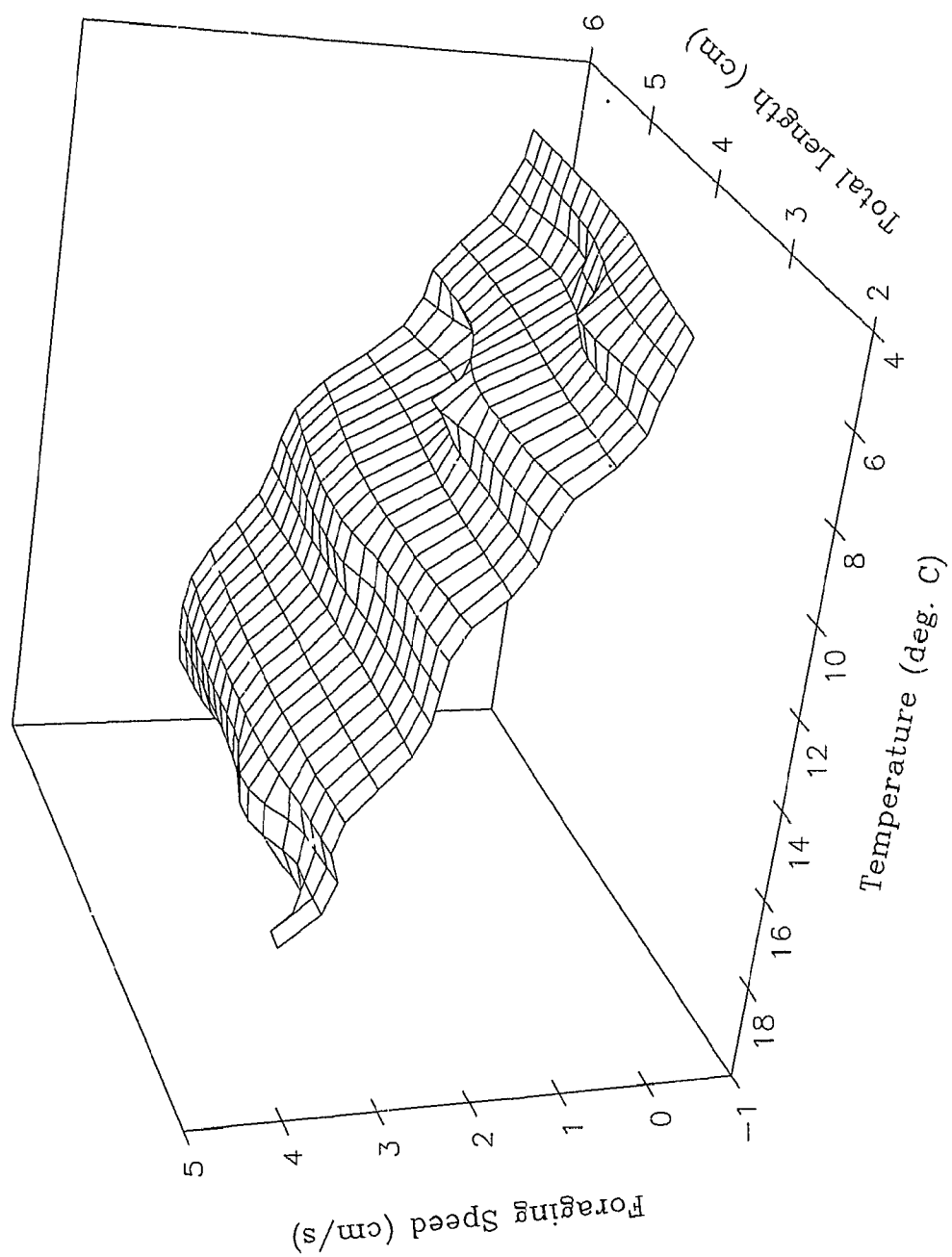


Fig. 2.2

Table 2.1. Energy budgets of (a) unfed and (b) fed 0+ cunner at three temperatures (5°C, 10°C and 15°C). The amount of energy ($\text{mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$) allocated to each activity was calculated as the metabolic cost of each activity (determined in Chapter 1), multiplied by the proportion of time spent on each activity. Resting metabolism = standard metabolic rate from y intercepts of Fig. 1.2. Foraging costs were calculated as the time spent swimming at a given speed (Fig. 2.2) multiplied by the energetic cost of swimming at that speed (Fig. 1.2), plus SDA (difference in elevation of fed vs unfed regressions in Fig. 1.2). Defense costs are assumed to be 95% of the active metabolic rate (see Fig. 1.7). The total metabolic cost is also presented as a percentage of scope for activity (from Fig. 1.5). n.d.: no data (fish did not feed at 5°C).

(a) unfed fish

	Temperature		
Activity	5°C	10°C	15°C
Resting	86.9	38.6	88.5
Foraging	5.7	102.2	78.5
Defense	4.6	18.0	18.0
Total	97.2	158.8	185.0
% Scope	2.7	17.0	14.3

(b) fed fish

	Temperature		
Activity	5°C	10°C	15°C
Resting	n.d.	56.0	131.3
Foraging	n.d.	138.5	104.5
Defense	n.d.	18.0	54.0
Total	n.d.	212.5	289.8
% Scope	n.d.	43.6	64.5

instantaneous level of apparent SDA in situ, energy budgets are presented for 'unfed' fish in Table 2.1a and for fish 'fed' to satiation in Table 2.1b. This analysis yielded a range of energy expenditures within which a fish in any state of digestion would fall. The cost of foraging was calculated from the slopes of the swimming regressions in Fig. 1.2 so as to include the costs of locomotion (based on swimming speeds derived from Fig. 2.2) and apparent SDA. Total metabolic costs increased with increasing temperature. Cunner operated at a much lower percentage of their aerobic scope at 5°C than at 10° or 15°C, primarily due to the large proportion of time spent resting at 5°C. Cunner appeared to spend less time foraging and more time resting in shelter at 15°C than at 10°C, but this was most likely a confounding effect of size, whereby younger, smaller fish settling in the warmer months required less food and spent more time sheltering, presumably in order to avoid predation.

Energy expenditure as a proportion of scope for activity did not differ significantly between 10°C and 15°C for unfed fish. However, fed fish consumed a larger fraction of their aerobic scope at 15°C than at 10°C (t-test, $t = 4.53$, $p < 0.05$).

Among-habitat variation in time budgets

Time budgets of 0+ cunner in four different habitats are shown in Table 2.2. Water temperature in all four habitats averaged approximately 15 C over the course of the study. The total time spent within the shelter site ranged from 36% on sandy bottom to 61% on rocky reefs. Analysis of variance indicated significant differences between habitats

Table 2.2. Time budgets of 0+ cunner inhabiting different habitat types in August and September, 1992. Water temperature was 15°C. The mean proportion of time (± 1 standard error) allocated to each activity was calculated from 10 successive 2 hr observation periods. Five individual cunner were observed in each period; the same individuals were not necessarily observed in successive observation periods.

Activity	Habitat			
	Reef	Cobble	Grass	Sand
Resting	.61 $\pm$.057	.57 $\pm$.034	.48 $\pm$.039	.36 $\pm$.027
Foraging	.32 $\pm$.018	.38 $\pm$.025	.49 $\pm$.032	.59 $\pm$.045
Defense	.07 $\pm$.011	.05 $\pm$.013	.03 $\pm$.015	.02 $\pm$.009

in the proportion of time spent in shelter ($F = 29.7$, $p < 0.001$). There was no significant difference in the time spent sheltering between rocky reef and cobble bottom (Tukey's HSD, $p > 0.05$). Cunner occupying Zostera beds spent less time in shelter than those inhabiting reefs or cobble bottom (Tukey's HSD, $p < 0.01$ for both cases), and cunner spent less time in shelter on sandy bottom (i.e. around pebbles, shell debris, or other small objects) than in any other habitat (Tukey's HSD, $p < 0.01$).

The total time spent foraging ranged from 32% on rocky reefs to 59% on sandy bottom. The difference between habitats was significant (ANOVA, $F = 42.5$, $p < 0.001$). Time spent foraging also did not differ between cunner on rocky reefs and cunner on cobble bottom (Tukey's HSD, $p > 0.05$). Cunner occupying Zostera beds spent significantly more time foraging than cunner on rocky reefs or cobble bottom (Tukey's HSD, $p < 0.05$ for both cases), and cunner on sandy bottom spent more time foraging than in any other habitat (Tukey's HSD, $p < 0.05$).

Time spent defending shelter sites ranged from 1.7% on sandy bottom to 7.3% on rocky reefs. There were significant among-habitat variations in time allocated to defense (ANOVA, $f = 37.4$, $p < 0.001$). As with shelter and foraging, there was no difference between rocky reef and cobble habitats in the time spent on defense (Tukey's HSD, $p > 0.05$). There was also no significant difference between Zostera beds and sandy bottom (Tukey's HSD, $p > 0.05$), although less time was allocated to defense in these habitats than on rocky reefs or cobble bottom (Tukey's HSD, $p < 0.01$). It appears from Table 2.1 that the amount of time spent on shelter site defense was directly related to the amount of time spent in the shelter.

Among-habitat variation in energy budgets

Energy budgets of 0+ cunner in each of four habitats are shown for 'unfed' fish in Table 2.3a and for fish 'fed' to satiation in Table 2.3b. For both fed and unfed fish (see Chapter 1), significant among-habitat differences were found in the allocation of energy to each activity (ANOVA, $F > 79.2$, $p < 0.01$ for all cases). Cunner inhabiting sand bottoms spent significantly more time foraging and less time resting in or defending shelter sites than did cunner on rocky reefs or cobble bottoms. The same was true of cunner inhabiting seagrass beds, although the difference was less marked. However, although there was a tendency for total energy expenditure and percentage of aerobic scope allocated to be higher on sand bottoms, the differences among habitats in total energetic cost were not statistically significant (ANOVA, $F = 2.7$, $p > 0.05$).

Effects of conspecific density on time budgets

The effects of three different density treatments on time budgets of 0+ cunner are shown in Table 2.4. The total time spent within the shelter site ranged from 54% on the high density reefs to 63% on low density reefs. Analysis of variance indicated significant differences between density treatments in the proportion of time spent in shelter ($F = 44.9$, $p < 0.01$). There was no significant difference in the time spent sheltering between low density and control reefs (Tukey's HSD, $p > 0.2$). Cunner occupying high density reefs spent less time in shelter than those inhabiting low density or control reefs (Tukey's

Table 2.3. Energy budgets of (a) unfed and (b) fed 0+ cunner inhabiting different habitat types in August and September, 1992. The amount of energy ($\text{mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$) allocated to each activity was calculated as per Table 2.1. n.d.: no data (fish did not feed at 5°C).

(a) unfed fish

Activity	Habitat			
	Reef	Cobble	Grass	Sand
Resting	94.7	88.5	74.5	46.6
Foraging	66.1	78.5	101.3	122.0
Defense	25.2	18.0	10.8	8.8
Total	186.0	185.0	186.6	197.4
% Scope	14.8	14.3	15.1	20.2

(b) fed fish

Activity	Habitat			
	Reef	Cobble	Grass	Sand
Resting	140.5	131.3	110.5	69.1
Foraging	88.0	104.5	134.7	162.2
Defense	25.2	18.0	10.8	8.8
Total	253.7	253.8	256.0	260.1
% Scope	47.2	47.3	48.3	50.3

Table 2.4. Time budgets of 0+ cunner subjected to different conspecific adult density treatments in August and September, 1992. Low density = 1 adult m⁻²; control = 2.4-3.2 adults m⁻²; high density = 5 adults m⁻². Observations were carried out on rocky reef habitats only. Water temperature was 15°C. The mean proportion of time allocated to each activity was calculated from 10 successive 2 hr observation periods (5 individuals per observation).

Activity	Density		
	Low	Control	High
Resting	.63 ± .087	.60 ± .073	.54 ± .086
Foraging	.37 ± .069	.28 ± .037	.18 ± .014
Defense	.01 ± .004	.12 ± .039	.28 ± .045

HSD, $p < 0.05$ for both cases).

The total time spent foraging ranged from 18% on high density reefs to 37% on low density reefs. The difference between treatments was significant (ANOVA, $F = 31.3$, $p < 0.01$). Time spent foraging differed significantly between all three density treatments (Tukey's HSD, $p < 0.05$ for all pairwise comparisons).

Time spent defending shelter sites ranged from $< 1\%$ on low density treatments to 28% on rocky reefs. There were significant differences between all treatments in time allocated to defense (ANOVA, $F = 114.5$, $p < 0.0001$; Tukey's HSD, $p < 0.01$ for all pairwise comparisons). Unlike the pattern exhibited among habitat types, it appears from Table 2.4 that the amount of time spent defending a shelter site was inversely related to the amount of time spent in shelter.

Effects of conspecific density on energy budgets

Energy budgets of 0+ cunner for each density treatment are shown for 'unfed' fish in Table 2.5a and for 'fed' fish in Table 2.5b. The proportion of energy spent in shelter did not differ significantly between density treatments (ANOVA, $F = 0.9$, $p > 0.05$). However, the proportion of energy spent on foraging was significantly higher (ANOVA, $F = 47.2$, $p < 0.01$) on low density reefs (Tukeys HSD, $p < 0.05$) and significantly lower on high density reefs (Tukeys HSD, $p < 0.05$) than on control reefs. The proportion of energy spent on shelter site defense differed drastically among density treatments (ANOVA, $F = 134.1$, $p < 0.0001$); the cost of defense was lower on low density reefs

Table 2.5. Energy budgets of (a) unfed and (b) fed 0+ cunner subjected to different conspecific density treatments in August and September, 1992. Low density = 1 adult m^{-2} ; control = 2.4-3.2 adults m^{-2} ; high density = 5 adults m^{-2} . The amount of energy ($\text{mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$) allocated to each activity was calculated as per Table 2.1.

(a) unfed fish

Activity	Density		
	Low	Control	High
Resting	97.8	93.1	83.8
Foraging	76.5	66.1	37.2
Defense	2.2	28.8	100.8
Total	176.5	188.0	221.8
% Scope	10.2	15.7	31.9

(b) fed fish

Activity	Density		
	Low	Control	High
Resting	145.1	138.2	124.4
Foraging	101.7	88.0	28.8
Defense	2.2	28.8	100.8
Total	249.0	255.0	274.7
% Scope	45.0	47.8	57.3

(Tukeys HSD, $p < 0.05$) and higher on high density reefs (Tukeys HSD, $p < 0.05$) than on control reefs. Energy spent on defense differed by two orders of magnitude between low density and high density treatments. Total metabolic cost (resting + foraging + defense) differed significantly among density treatments (ANOVA, $F = 34.5$, $p < 0.01$) and was greater on high density reefs than on low density reefs (Tukeys HSD, $p < 0.05$).

Diel patterns of activity

The diel cycle of activity of 0+ cunner in September, 1991 is shown in Fig. 2.3. Cunner were assumed to be torpid during the hours of dark (Olla et al. 1975). Soon after sunrise, cunner began to leave their shelter sites for short bouts of activity. Time spent in shelter decreased from 100% of the total time budget at dawn (0500-0600 hrs) to about 60% at 0900 hrs, where it remained constant until the late afternoon. From 1400 to 1700 hrs, the time allocated to shelter decreased to a minimum of 20%, after which it increased rapidly to 100% of the budget as cunner assumed their torpid state for the night. Foraging increased from 0% of the time budget at dawn to a morning peak of 35% from 0800 to 0900 hrs, then decreased to approximately 25% through the hours of 0900 to 1200, before reaching a mid-afternoon peak of approximately 50% of the budget from 1500 to 1600 hrs. After 1600 hrs, the time allocated to foraging steadily declined, reaching 0% at or around 1800 hrs. The time allocated to shelter site defense rose from 0% at dawn to 10% at noon, where it thereafter oscillated until 1700 hrs, when it abruptly increased to 30%. Time spent on defense increased further to 45% of the time

Fig. 2.3. Diel time budget for 0+ cunner at 15°C, in rocky reef habitats. Proportion of time allocated to each activity is presented on an hourly basis for a representative 24 hr period. The mean proportion of time allocated to each activity was calculated from 10 successive 2 hr observation periods (5 individuals per observation) in August and September, 1992. Vertical error bars represent ± 1 standard error.

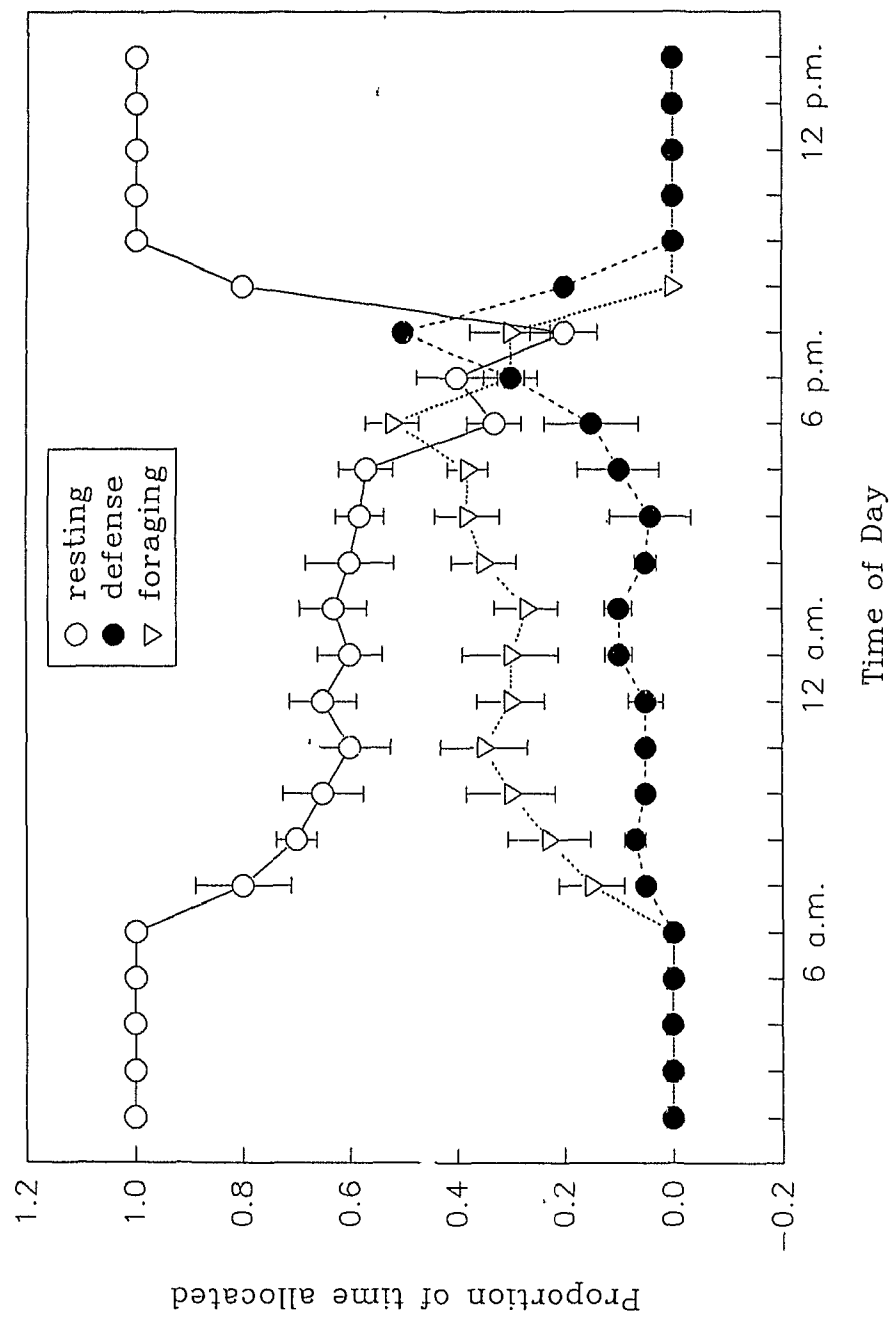


Fig. 2.3

budget from 1700–1800 hrs, as cunner fought over shelter sites in which to spend the night (personal observations). After sunset, defense time abruptly dropped to 0% as cunner entered the torpid state.

Diel patterns in energy allocation

Daily energetic costs of resting, foraging and shelter site defense at 15°C were calculated using data from Chapter 1. Energetic expenditures on an hourly basis from sunrise to sunset are shown in Fig. 2.4 for 'unfed' fish and Fig. 2.5 for 'fed' fish. Total energy expenditure tended to increase throughout the day, reaching a peak in late afternoon, shortly before sunset. This peak resulted from the dual loads of foraging and acquiring/defending a nocturnal shelter site. The maximum cost of these activities rose to > 56% of the scope for activity in unfed fish and > 70% in fed fish.

DISCUSSION

The allocation of energy between activities associated with maintenance and growth has profound implications for the survival and eventual reproductive success of fish (Wootton 1990). However, there is little or no information on how energy allocation is regulated in response to the abiotic and biotic environment of fish. Priede (1985) suggested that the probability of dying increases the longer a fish expends energy at or near the standard (minimum) or active (maximum) metabolic rate. A fish should thus

Fig. 2.4. (a) Diel cycle of energy expenditure for 'unfed' 0+ cunner at 15°C, in August and September, 1992. Energetic cost (measured as oxygen consumption ($\text{mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$)) of each activity was calculated as per Table 2.1. (b) Diel energy expenditure expressed as a percentage of scope for activity.

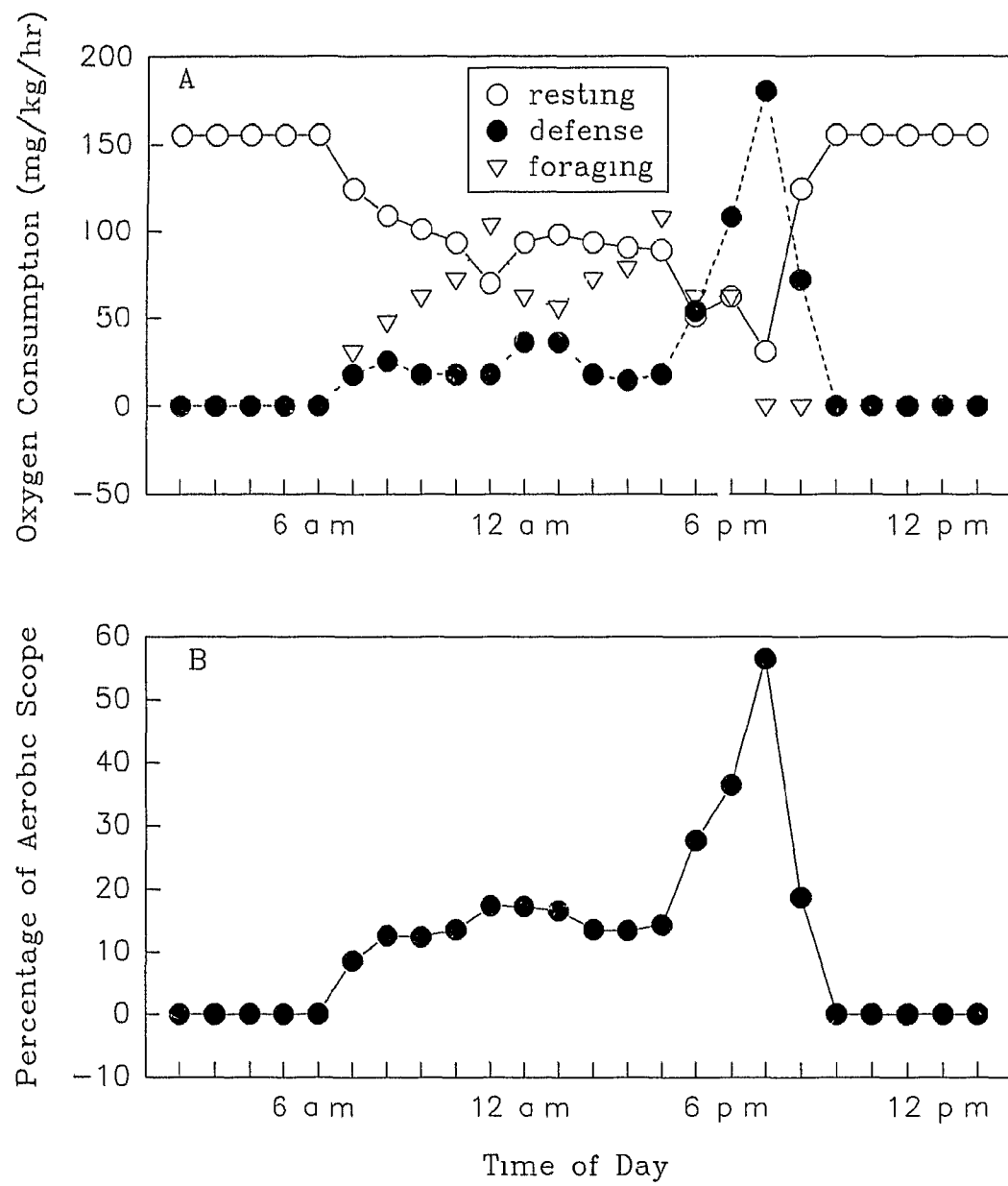


Fig. 2.4

Fig. 2.5. Diel cycle of energy expenditure for 'fed' 0+ cunner at 15°C, in August and September, 1992. Energetic cost (measured as oxygen consumption ($\text{mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$)) of each activity was calculated as per Table 2.1. (b) Diel energy expenditure expressed as a percentage of scope for activity.

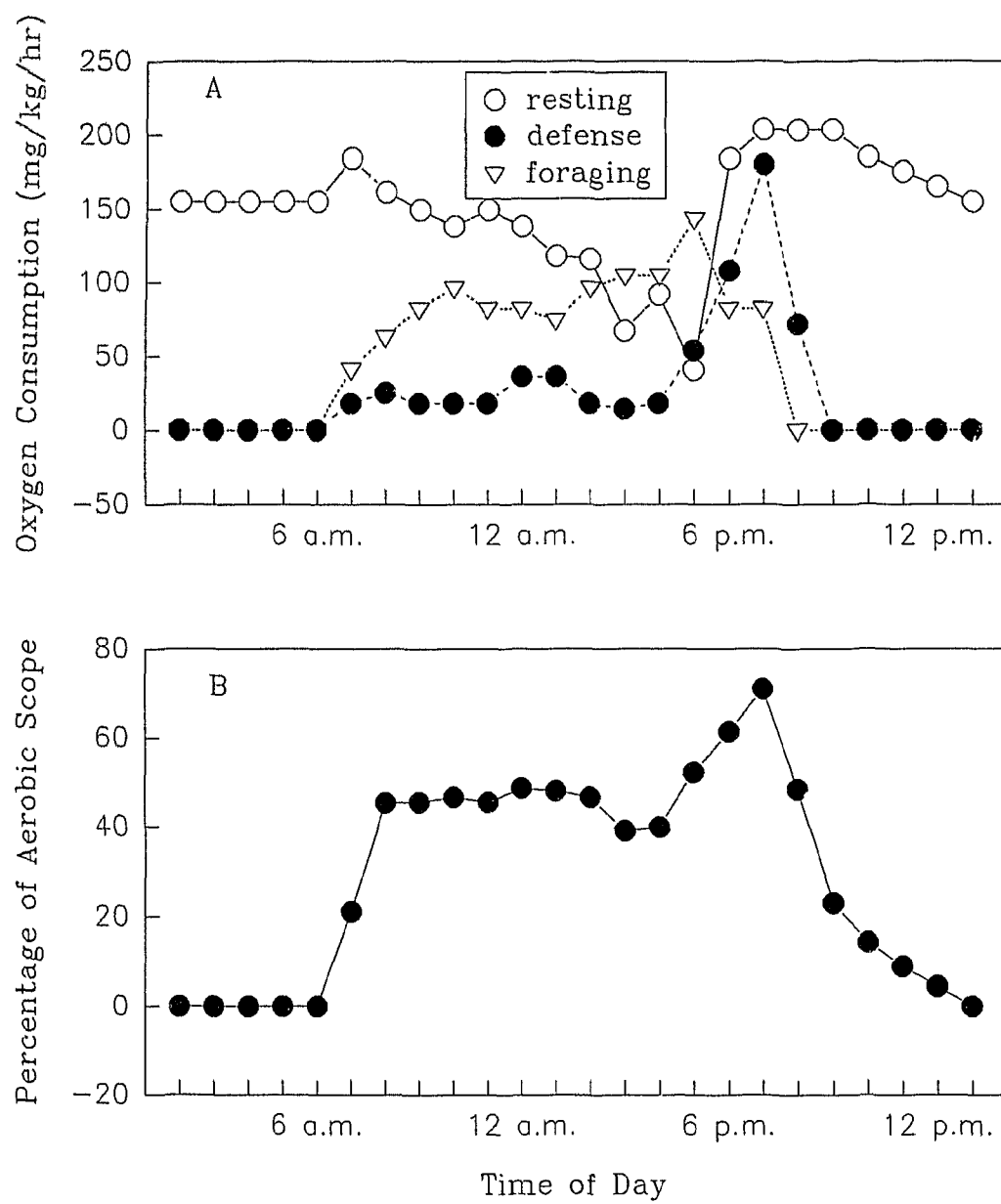


Fig. 2.5

regulate its energy expenditure so that normal activities, such as foraging and shelter site defense, will have a low probability of exceeding the scope for activity (Wootton 1990). Telemetric studies of pike (Esox lucius), brown trout (Salmo trutta) and Atlantic cod (Gadus morhua) show that the metabolic cost of locomotion is kept low (Diana et al. 1977; Soofiani and Hawkins 1985). The primary advantage of operating at a low level of activity is that for a given energy (i.e. caloric) intake, more energy can be directed to growth or gamete production (Wootton 1990). Boisclair and Leggett (1989a) found that activity accounted for 0-40% of the energy budget of yellow perch (Perca flavescens), while apparent SDA accounted for 15-17%. They suggested that growth should be negatively correlated with activity costs. Koch and Wieser (1983) reported that a reduction in swimming by roach over a six month period resulted in an energy savings of 1485 kJ per kg of fish. During this period, 364 KJ of gonadal tissue per kg of fish was synthesized.

In this study, cunner appeared to keep their metabolic expenditure relatively low throughout most of the day. The percent of scope for activity expended by newly settled cunner ranged from about 14% to 50% (with short late afternoon peaks of 50-70%), depending on digestive state (Table 2.2a,b; Table 2.7a,b). However, juvenile fish are known to exhibit rapid growth (Weatherly and Gill 1987), and cunner spent roughly equal proportions of time foraging (32-59%) or resting (36-61%), depending on habitat type (Table 2.1). In contrast, adult male hummingbirds (Eulampis jugularis and Calypte anna) spend 76-88% of their daily time budget on sitting at rest, and only 5-21% on foraging (Wolf and Hainsworth 1971).

Effects of temperature and body size on time and energy budgets

Temperature and body size had a complex interactive effect on the ecological energetics of cunner. While ontogenetic changes in behaviour may affect the allocation of time to various activities (Krebs and Davies 1984), the energetic cost of each activity, as well as the metabolic scope for activity, are dependent on temperature (Brett and Groves 1979).

At temperatures above 10°C, time budgets appeared to be regulated by body size more than temperature (Fig. 2.1). Since rates of enzyme-catalysed reactions and therefore metabolic rates increase with temperature (Dreidzic and Hochachka 1978; Hochachka and Somero 1984), animals may be expected to forage more at higher temperatures. However, as newly settled fish are particularly susceptible to predation (Sale and Ferrell 1988; Hixon and Beets 1993; Juanes 1994), they may spend more time in shelter rather than actively foraging (time-minimizing strategy). As cunner grow, they will become less susceptible to size-selective piscivory (Juanes 1994), and may therefore spend less time in shelter and more time foraging (energy-maximizing strategy); which would be necessary to maintain their larger body size and to accelerate the onset of sexual maturity. This is of particular importance to cunner, which reach sexual maturity as a function of size (54-60 mm) rather than age (Dew 1976). In order for cunner to spawn in their second summer (age 1+), they must approach this size the preceding winter, since cunner survive overwinter on stored energy and do not grow (Auster 1989). If cunner do not approach the requisite size for sexual maturity before the onset of torpor, they may not

spawn until their third summer (Dew 1976); this may represent a significant reduction in fitness over the 5-6 year lifespan of the animal.

It is unknown whether other fish species undergo similar ontogenetic shifts in energy allocation strategy, but it seems likely that many temperate demersal fishes may attempt to keep activities that expose them to predation to a minimum, until the fish outgrow the most vulnerable size classes. At that point, somatic and gonadal growth may become more important factors than predation risk in determining patterns of energy allocation.

At temperatures below 10°C, temperature became more important than body size in determining activity patterns of cunner (Fig. 2.1). As temperature decreased in early winter, cunner spent less time on all activities and more time resting in shelter, eventually becoming torpid throughout the diel cycle. Cunner have a much lower scope for activity at 5°C than at 10°C or 15°C (Fig. 1.5). However, their activity levels at 5°C are so strictly curtailed that they actually operate at a much lower percentage of their metabolic scope than at warmer temperatures (Table 2.1a,b). Priede (1985) found that although brown trout (*Salmo trutta*) had a lower scope for activity at 5.5°C than at 15°C, the depressed appetite and consequent reduction in foraging activity at the lower temperature resulted in a much lower proportion of the metabolic scope being expended during normal activity.

Effects of habitat on time and energy allocation

In order for defense of shelter sites to evolve as a behaviour, shelter must be a

limiting resource which is economically defensible (Brown 1964). In other words, selection can favour the maintenance of shelter sites only if the benefits gained, in terms of energy savings from resting within the shelter coupled with reduced predation risk, outweigh the cost of shelter site defense. Based on their patterns of energy allocation, animals may be broadly categorized as 'time-minimizers' or 'energy-maximizers' (Schoener 1971; Hixon and Carpenter 1988). Time-minimizers are those animals which minimize the time spent on foraging or shelter site defense and so allow more time for resting. This strategy confers an energy saving, which can then be allocated to somatic or gonadal growth. For newly settled fish, an additional advantage of time-minimizing would be a reduction in predation risk, as less time is spent exposed in active behaviours. Energy-maximizers are those animals which maximize the time spent on foraging in order to directly maximize somatic and/or gonadal growth. Small juvenile fish may employ an energy maximizing strategy in order to reduce the time spent in smaller, more vulnerable size classes (Juanes 1994) and/or attain earlier social dominance (Tupper and Boutilier 1992, 1994).

Although habitat type had no significant effect on the total metabolic rate or the percentage of aerobic scope expended, it had a notable influence on the allocation of time and energy to resting, foraging and shelter site defense. Cunner occupying rocky reefs and cobble bottoms appeared to optimize their time budgets, spending 57-61% of their time resting in shelter, while cunner inhabiting sandy bottoms spent 49-59% of their time foraging and thus appeared to maximize their energy intake (Table 2.3). Cunner inhabiting seagrass beds spent roughly equal amounts of time on resting and foraging and

could not easily be categorized as either time-minimizers or energy-maximizers (Table 2.2).

The type of strategy utilized by cunner in a given habitat may be related to the quality and quantity of shelter sites offered by that habitat. Thus, cunner on reefs and cobble bottoms, which provide large numbers of high-quality shelter sites (see Chapter 4), may spend a larger proportion of their time sheltering where they can avoid predation and simultaneously reduce their energy expenditure. Cunner on sand bottoms, which provide low numbers of poor-quality shelter sites (see Chapter 4), may maximize the time spent foraging, in order to grow more quickly and thus avoid size-selective predation (Juanes 1994). Since seagrass beds provide shelter sites of intermediate quality, the strategy employed by cunner in this habitat may be seen as lying on a continuum, the opposing ends of which are time-minimizing and energy-maximizing. This, however, assumes that food quality and quantity are not sufficiently different between habitats to decouple foraging time and growth (see Boisclair and Leggett 1989a,b).

Effects of conspecific density on time and energy budgets

Conspecific density had a profound effect on the allocation of energy among daily activities (Table 2.5a,b). The amount of time and energy spent on foraging by cunner on high density reefs was half that on low density reefs, while both the time and energy spent on shelter site defense increased by a factor of >50 from low to high density reefs. Boisclair and Leggett (1989b) found that growth of 0+ yellow perch (Perca flavescens)

was inversely related to fish density, and hypothesized that the lower growth rates were caused by increased rates of activity at higher densities. Li and Brocksen (1977) found that routine metabolic rate increased and growth decreased with increasing stocking density of juvenile rainbow trout (Onchorhyncus mykiss) in an artificial stream. In cunner, however, the time spent on activity as opposed to resting did not differ greatly between density treatments (Table 2.2). The difference in total expenditure arose from a shift in energy allocation from foraging activity to more expensive shelter site defense at high density. Thus one might predict a negative relationship between growth of 0+ cunner and conspecific density, due to the greater energy expenditure and reduced time spent feeding at higher densities.

Ware (1982) has stated that the surplus energy acquired by a fish is a complex function of food availability, in which a limited supply can result in various compensatory behaviours involving foraging patterns, swimming speeds, or defense of a feeding territory. At high densities, these behaviours cannot adequately compensate for resource limitation, so individual rates of energy uptake decrease, resulting in density-dependent growth. This same argument can be applied to shelter sites, which at high densities can be a limiting resource (Shulman et al. 1983; Shulman 1984, 1985a,b). The results of this study have demonstrated that a decrease in shelter site availability leads to an increase in individual rates of energy expenditure, which in terms of surplus power is functionally equivalent to a decrease in energy uptake.

Diel patterns of time and energy allocation

Diel patterns of activity have mostly been studied in coral reef fishes, due to the ease of observation in these systems (Hobson 1972, 1973; Helfman 1986). However, no concurrent investigations of energetic costs have accompanied studies of diel activity of fishes.

Many species, including cunner, vary the amount of time allocated to various activities throughout the diel cycle (Helfman 1978, 1986; this study). For example, foraging may occur mainly during the daylight hours, at night, or at dawn and dusk (Helfman 1986). Within these broad categories, some activities may take place over a much more limited period. Hobson (1973) observed that some large piscivorous fishes on coral reefs foraged actively for about 20 minutes around the time of sunset, when smaller fish leaving the water column were silhouetted against the acute angle of light from the setting sun. In this study, cunner were active throughout the day (Fig. 2.3), but foraging was most prevalent in the late afternoon. Foraging activity remained relatively low throughout the morning and early afternoon; this may be a mechanism by which cunner avoid a high SDA, which might restrict their ability to acquire and/or defend a shelter site, thus increasing predation risk. Shelter site defense peaked shortly before sunset, as cunner competed to acquire or maintain sleeping sites. The peak of activity late in the day could account for up to 71% of the scope for activity (Fig. 2.5).

Interestingly, the peak of foraging occurred roughly 2-3 hrs before the onset of torpor, at which time apparent SDA would be at or near its maximum amplitude (Chapter 1).

It is possible that the nocturnal torpor of cunner may have evolved as a mechanism to offset the high energetic cost of the combined late-day peaks of foraging and shelter site defense. Although metabolic suppression is usually seen as a response to drastic environmental change (Storey and Storey 1990), there is no reason why it should not function on a spatio-temporally more restricted scale (Wieser 1989), such as the daily torpor that occurs in many birds and small mammals. Since torpor can reduce the standard metabolic rate of cunner by $> 20\%$ (Chapter 1), it may confer an energy surplus which could then be allocated to somatic or gonadal production.

Summary and Conclusions

In conclusion, it appears that age 0+ cunner may adopt a number of energy allocation strategies, depending on abiotic and biotic factors such as habitat type, temperature, body size and crowding. Smaller fish which are more vulnerable to predation, or those fish which have access to high quality shelter, will tend to minimize the time and energy spent on activity. Larger fish, or those without access to high quality shelter, will tend to maximize their net energy intake by allocating more time and energy to foraging.

High densities of conspecifics greatly increased the amount of time and energy allocated to shelter site defense, while reducing foraging activity. Thus an energy deficit from the cost of defense, coupled with a decreased feeding rate, should lower growth rates of cunner at high population densities, as has been found for several species of reef fish (Doherty 1982, Forrester 1990, Jones 1991). Further research is needed to test this

hypothesis.

Since the total energy expenditure and percentage of scope for activity did not vary between habitats, it is unclear what effect habitat type will have on growth of 0+ cunner. Assuming equal prey quantity and quality between habitats, one might expect higher growth rates in sand and seagrass habitats, due to the increased foraging time (Table 2.2). However this increased growth may be offset by higher mortalities in sand and seagrass habitats, where cunner spend less time in shelter. Trade-offs between growth and mortality in different habitats are a subject of great interest to ecologists (Gilliam and Fraser 1987; Gotcietas 1990; Sogard 1992; Walters and Juanes 1994). Combining information on energetics with studies of settlement, mortality and growth of age 0+ juveniles may help us to clarify processes leading to recruitment variation in demersal fishes.

CHAPTER 3

EFFECTS OF CONSPECIFIC DENSITY ON SETTLEMENT, GROWTH AND POST-SETTLEMENT MORTALITY OF A TEMPERATE REEF FISH

INTRODUCTION

Reef fishes, like many marine organisms, possess a planktonic larval stage characterized by widespread dispersal and extreme mortality. After a period of planktonic life, the larva settles to a substrate and is considered a recruit to the benthic (or demersal) population. One of the central problems in marine ecology is to determine the relative importance of pre-settlement and post-settlement processes in the regulation of populations. Over the past 2 decades, a progression of models has been developed to explain the variability in the abundance and structure of reef fish populations (Doherty 1982, 1983; Shulman et al. 1983; Victor 1983, 1986; Shulman 1984, 1985a; Shulman and Ogden 1987; Doherty and Williams 1988; Forrester 1990; Jones 1990; Levin 1993, 1994a,b; Doherty and Fowler 1994). Early models were preoccupied with the effects of competition and predation on resident reef fish. These models predicted an excess of recruitment and a temporally stable adult population regulated by density-dependent competition for limited resources (Smith and Tyler 1972; Sale 1977, 1978; Smith 1978;

Shulman 1984, 1985a). Later models argued that population size of reef fish was determined by pre-settlement processes limiting the supply of larvae. The prediction in this case was that recruitment would be independent of adult density, and that adult population size and structure should directly reflect patterns of recruitment (Doherty 1982, 1983; Victor 1983, 1986; Doherty and Williams 1987). Recently, a more multifactorial approach has been suggested, the goal of which is to assess the relative importance of pre-settlement and post-settlement processes in structuring reef fish populations (Shulman and Ogden 1987; Connell and Jones 1991; Hunt von Herbing and Hunte 1991; Jones 1991; Levin 1993, 1994a,b; Doherty and Fowler 1994; Tupper and Hunte 1994).

Variations in post-settlement mortality and growth have been identified as potentially important processes regulating population structure and abundance (Jones 1991). Mortality of reef fishes can vary substantially; both size/age-specific mortality and habitat-specific mortality have been demonstrated (Eckert 1987; Shulman and Ogden 1987; Sale and Ferrell 1988; Connell and Jones 1991; Levin 1993, 1994a,b). In general, mortality is extremely high in the first days or weeks following settlement (Shulman and Ogden 1987; Sale and Ferrell 1988; Jones 1991; Levin 1993, 1994a), and even small variations in the rate of mortality are capable of modifying patterns of recruitment to the extent that variations in larval settlement are no longer reflected in the adult population (Doherty 1991; Jones 1991; Levin 1994a).

Growth rates of newly settled fish may also be highly variable (Connell and Jones 1991). Growth rate may affect population size indirectly through size-specific predation concentrating on smaller size classes of prey (Post and Evans 1989), or directly by

limiting the number of individuals reaching sexual maturity, the latter being an important factor in the regulation of adult population size (Jones 1987a). Since sexual maturity in many reef fishes appears to be size-dependent rather than age-dependent (e.g. Dew 1976, Jones 1987a), the number of individuals reaching maturity will be a function of the combined effects of settlement strength, postsettlement mortality and growth rate (Jones 1984, 1987a). These processes may be strongly influenced by intraspecific competition for limited resources, resulting in density-dependent mortality and growth. While Jones (1987a) found no effect of adult Pomacentrus amboinensis on survivorship of conspecific juveniles, he found that growth rate and maturation were depressed in the presence of adults. Similar results have been reported for other species (Doherty 1982, 1983; Victor 1986). Hunt von Herbing and Hunte (1991) and Tupper and Hunte (1994) found evidence for density-dependent settlement and/or post-settlement mortality in 3 species of Caribbean reef fish. While the demonstration of density-dependent effects is evidence for competition, it does not identify the resources for which fish are competing (Jones 1987a). Density-dependent growth may result from limited food supply (Thresher 1983; Jones 1986; Forrester 1990) or from direct social inhibition (Jones 1987a,b, 1990; Forrester 1990; Tupper and Boutilier 1994). In the latter case, energy is directed away from foraging and growth and toward agonistic interactions, such as shelter site defense (see Chapter 2). Cunner (Tautoglabrus adspersus) spent 50 times more energy competing for shelter sites at population densities of 5 fish m⁻² than at densities of 1 fish m⁻² (Fig. 1.7, Table 2.5).

The purpose of this study is to assess the relative importance of settlement and post-

settlement processes (mortality and growth) to the population dynamics of cunner, and to determine the effects of resident population density on these processes. I adopted an experimental approach in which settlement, post-settlement mortality and growth rate of age 0+ cunner were monitored on reefs on which either adult or recruit density had been artificially increased or decreased. Previous studies of the relative importance of settlement and density-dependent post-settlement processes have primarily employed small artificial reefs (Shulman et al. 1983; Shulman 1984, 1985; Jones 1986, 1987a,b, 1988; Forrester 1990; Levin 1993, 1994a), which may have affected the validity of their results with respect to natural populations (Doherty 1991). We used natural reefs of approximately equal size and structure in order to escape any effects of artificial habitat.

METHODS

The study was conducted at Back Cove on St. Margaret's Bay, Nova Scotia. This area is characterised by granite bedrock exposed by heavy glaciation. Exposed bedrock below the subtidal zone forms a series of rocky reefs. In addition, glacial erratics (large, isolated granite boulders deposited as glaciers retreated) are common both above and below the tideline. These erratics form an isolated fish habitat analogous to coral patch reefs in tropical oceans. In each of two experiments, a group of 12 boulders, situated at a depth of 2-3 m and isolated from each other by at least 20 m, were chosen as study reefs.

Experiment 1: Effects of adult density on settlement, postsettlement mortality and growth

In August, 1992 (prior to the start of the settlement season), a group of 12 boulder reefs, similar in size and structure, was randomly divided into 3 sets of 4 reefs. Population density of resident cunner (age 1+ and older) on the first group ("high density reefs") was artificially increased to 5 individuals m^2 , while density on the second group ("low density reefs") was reduced by removal to 1 individual m^2 . The remaining group ("control reefs") was untreated, and supported natural densities of 2.4 to 3.2 newly settled individuals m^2 . Visual censuses of these reefs were conducted at weekly intervals from July 1 to Oct 29, 1992. From mid-August to early September (the settlement season for cunner in this area), newly settled cunner were collected daily using the anaesthetic Quinaldine, measured to the nearest mm and marked with waterproof acrylic paint. A system of different dot patterns and colors was used to identify individuals. At the end of the settlement period in late August, again in late September, and a third time at the end of October, all remaining 0+ cunner were recaptured and remeasured. The growth increment of each individual was divided by the number of days since settlement to arrive at a daily rate of growth.

Recruitment success was defined as the density of 0+ cunner remaining at the end of October. Post-settlement survivorship was calculated by dividing recruitment success by the total number of settlers, and was expressed as a percentage (i.e. the percentage of marked individuals that were recaptured). It can be safely assumed that emigration was not a significant factor in the disappearance of young cunner from their home reef.

Juvenile cunner are very site-attached; no unmarked immigrant juveniles were observed on the study reefs and regular surveys of the area surrounding each study reef did not reveal any evidence of emigration. Indeed, all recaptures of 0+ cunner took place within 1 m of the original point of capture. Age 1+ and older cunner were transplanted from reefs at least 2 km from the study site to reduce the possibility of emigration to their home reef (Olla et al. 1979).

Settlement, recruitment success and growth rate were compared between treatments using analysis of variance. Prior to analysis, data were tested for homogeneity of variance using Bartlett's Test (Wilkinson 1990) and transformed where necessary to ensure homoscedasticity. Where significant differences between means occurred, their location was determined by post-hoc multiple comparisons (Tukey's HSD; Wilkinson 1990).

Experiment 2: Effects of recruit density on mortality and growth

As in experiment 1, a group of 12 reefs was randomly divided into 3 sets of 4 reefs. In October, 1992 (after the settlement season), all cunner of age 1+ or older were removed from the reefs. Population density of 0+ cunner on the high density reefs was artificially increased to 10 individuals m^{-2} , while on the low density reefs, the number of cunner was reduced to 3 individuals m^{-2} . The control reefs supported natural densities of 4.9 to 6.3 individuals m^{-2} . Techniques for visual census and estimation of mortality and growth were performed as described for Experiment 1 above.

RESULTS

Experiment 1

Settlement of cunner on the study reefs occurred over a 12 day period in August. On all reefs, newly settled cunner aggregated in small groups for 3-4 days post-settlement. During this time, each group appeared to share a shelter site which was usually insufficient to accommodate all members of a group. Within 5-7 days post-settlement, all such groups had dispersed, and each individual occupied and defended its own shelter site.

Settlement did not differ significantly between treatments (ANOVA, $F = 0.7$, $p > 0.05$; Figs. 3.1, 3.2a). However, survival of newly settled cunner (Fig. 3.2b) on the low density reefs (mean = 26.9%) was significantly higher than on the control reefs or the high density reefs (ANOVA, $F = 141.7$, $p < 0.001$). On the high density reefs, no 0+ cunner remained at the end of October (Fig. 3.1). Survival was higher on the control reefs (mean = 6.8%). The variation in mortality between treatments was sufficient to completely alter the pattern of settlement. As a result of this variation, recruitment success differed significantly between treatments (ANOVA, $F = 214.9$, $p < 0.0001$). Recruitment strength was high on the low density reefs, low on the control reefs, and zero on the high density reefs. Pairwise comparisons of treatment means revealed significant differences in recruitment between all 3 treatments (Tukeys' HSD, $p < 0.05$).

Growth rates of newly settled cunner were significantly higher on the low density

Fig. 3.1 Decline in population abundance of 0+ cunner from July through October, 1992, for each of three adult density manipulation treatments. Low density: adult density artificially reduced to 1 m⁻²; Control: adult density unmanipulated; High density: adult density artificially increased to 5 m⁻². Vertical error bars represent ± 1 standard deviation.

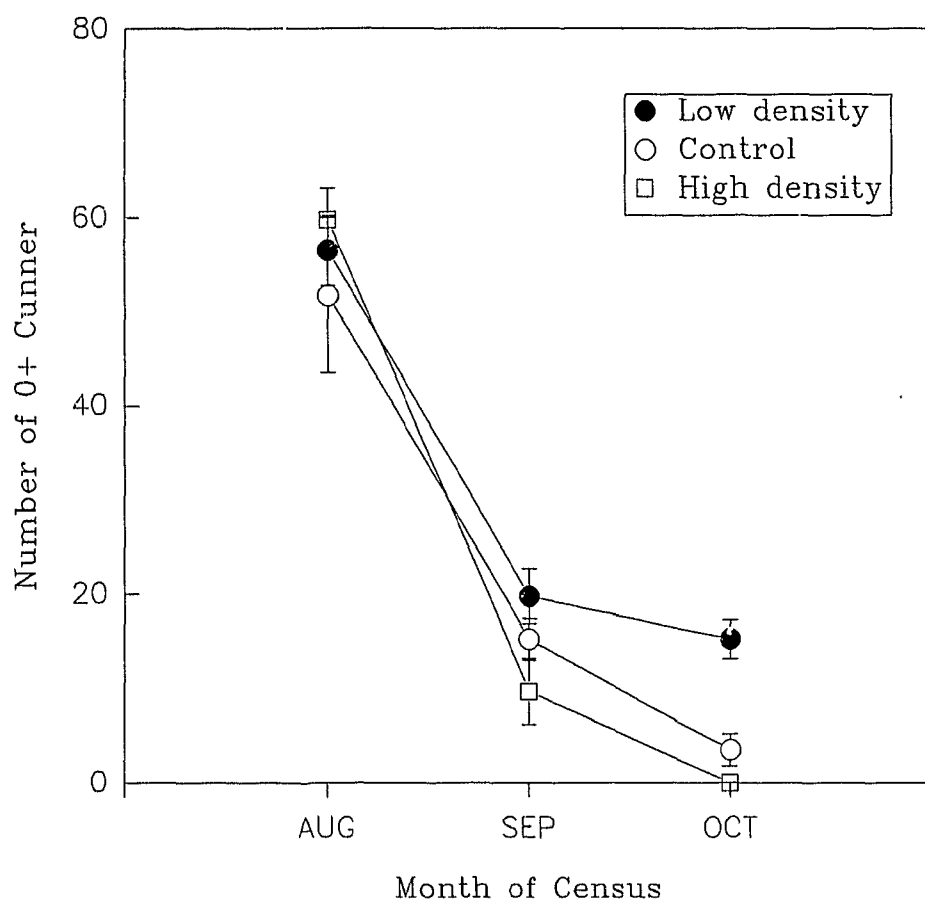


Fig. 3.1

Fig. 3.2 Effects of adult conspecific density on (a) settlement, (b) post-settlement survival, and (c) growth rate of 0+ cunner. Low density: adult density artificially reduced to 1 m⁻²; Control: adult density unmanipulated; High density: adult density artificially increased to 5 m⁻². Vertical error bars represent ± 1 standard deviation.

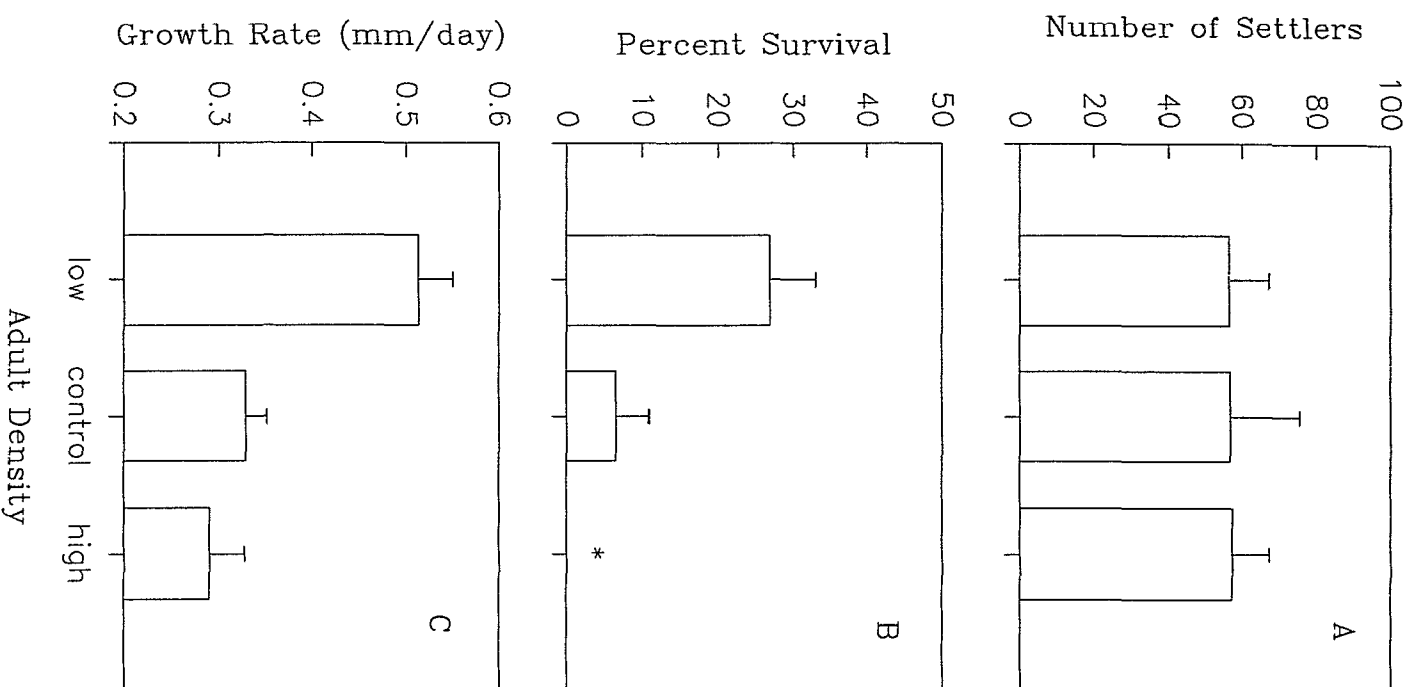


Fig. 3.2

reefs than on the high density or control reefs (ANOVA, $F = 28.9$, $p < 0.05$; Fig. 3.2c), although there was no significant difference in growth rate between the high density and control reefs (Tukeys' HSD, $p > 0.05$). This suggests that growth of cunner in Back Cove is density-dependent.

On all study reefs, regardless of adult density, size-dependent dominance hierarchies among newly-settled cunner were evident by the first recapture in September. By this time, 0+ cunner on all reefs were graded in size, and in no case did any individual overtake another in size. The rank size of each individual at the end of the settlement season was strongly correlated to its rank size in late September ($r_s = 0.8$, $p < 0.05$; Fig 3.3a) and in late October ($r_s = 0.9$, $p < 0.05$; it was not possible to relate size in late August to size in late October for the high density treatment, as no 0+ cunner survived to late October on the high density reefs). The rank growth rate of individual cunner was also positively correlated with size at settlement ($r_s = 0.9$, $p < 0.05$; Fig. 3.3b). Moreover, by following marked individuals, it was possible to investigate size-specific post-settlement survival. In order to determine size-specific survival of natural populations, settlers (8–14 mm total length) from the control reefs were grouped into 1 mm size classes; the number of survivors in each size class was then divided by the total number of settlers. Post-settlement survival was positively correlated with size at settlement ($r_s = 0.7$, $p < 0.05$; Fig. 3.4).

Fig. 3.3 Effects of rank size at settlement on (a) rank size at the end of September (i.e. post-recruitment size) and (b) rank growth rate of 0+ cunner. Data are for all treatments pooled. Tied ranks are averaged.

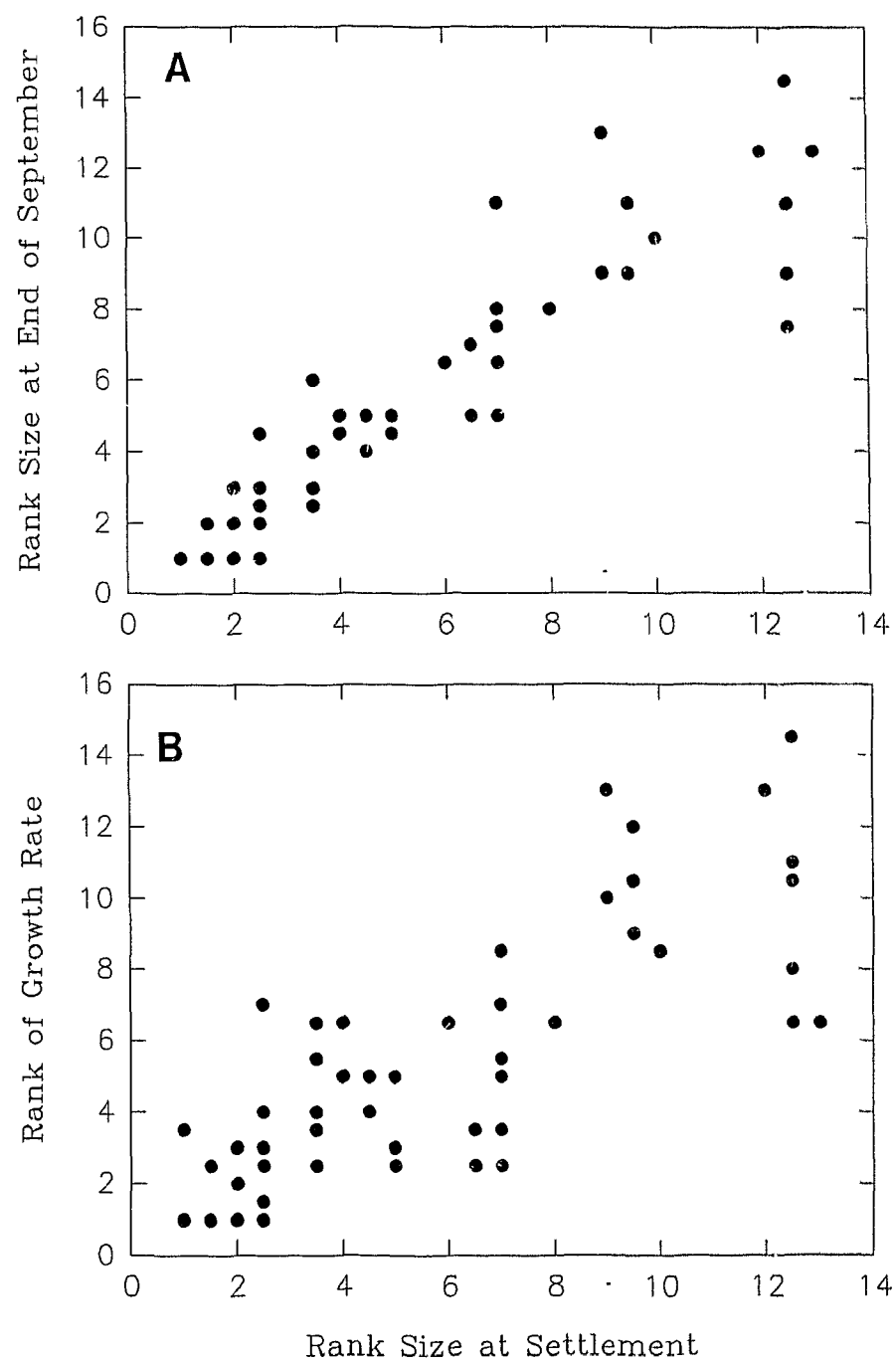


Fig. 3.3

Fig. 3.4 Effects of size at settlement on percent post-settlement survival of 0+ cunner. Survival was calculated for each 1 mm size-class of settlers as the proportion of total settlers remaining in November. Data are for control reefs only.

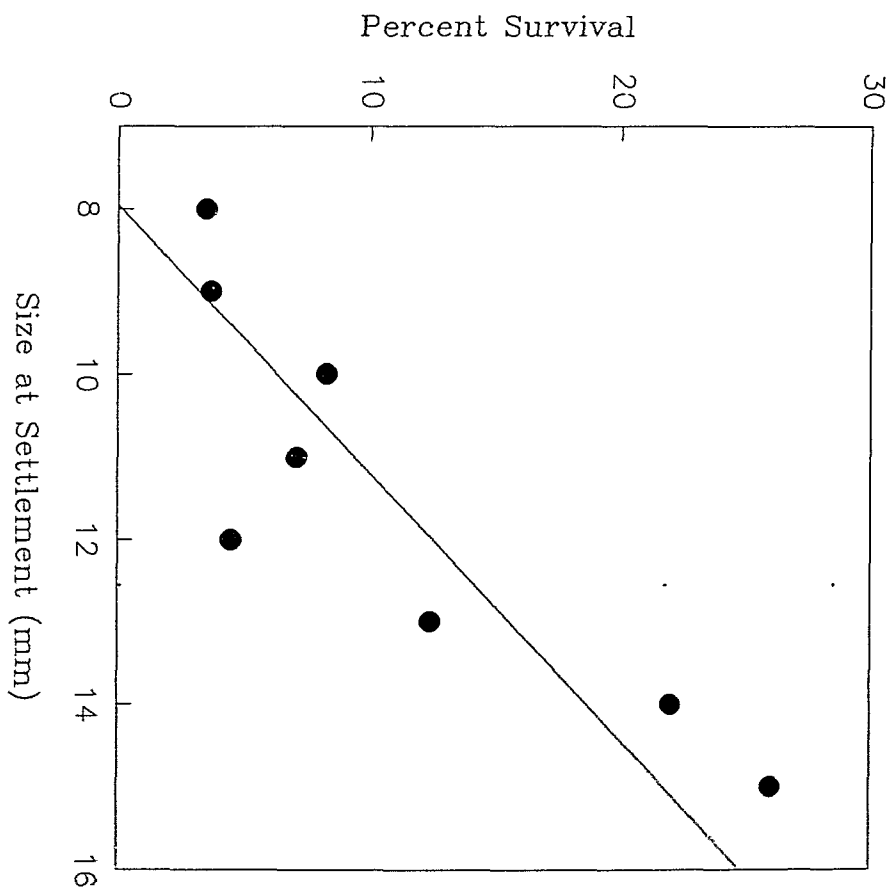


Fig. 3.4

Experiment 2

All cunner of age 1+ or older were removed prior to this experiment, so that only 0+ fish were present (see Methods). The decline in population density from August to October is shown in Fig. 3.5. Significant differences in post-settlement survival were again found between density treatments (Fig. 3.6a). Survival of 0+ differed significantly between all density treatments (ANOVA, $F = 71.9$, $p < 0.001$; Tukeys' HSD, $p < 0.01$ for all pairwise comparisons). Survival was again highest on the low-density reefs (32%). Survival on the control reefs (mean = 8.9%) and high density reefs (mean = 2.9%) was significantly higher than in the presence of older fish in Experiment 1 (t-test, $t = 5.2$, $p < 0.05$ for control reefs; $t = 14.3$, $p < 0.01$ for high density reefs). Interestingly, recruitment success in this experiment did not differ between treatments (ANOVA, $F = 0.9$, $p > 0.5$), as the density of 0+ cunner reached similar values on all reefs by December (Fig. 3.3).

Figure 3.6b shows that growth rates of 0+ cunner differed significantly between all density treatments (ANOVA, $F = 87.2$, $p < 0.001$; Tukeys' HSD, $p < 0.05$ for all pairwise comparisons). Growth was again highest on low density reefs and lowest on high density reefs. This suggests that growth of 0+ cunner can be depressed by high densities of conspecific recruits as well as the presence of adults.

Fig. 3.5 Decline in population abundance of 0+ cunner for each of three recruit density manipulation treatments. Low density: recruit density artificially reduced to 3 m⁻²; Control: recruit density unmanipulated; High density: recruit density artificially increased to 10 m⁻². Vertical error bars represent ± 1 standard deviation.

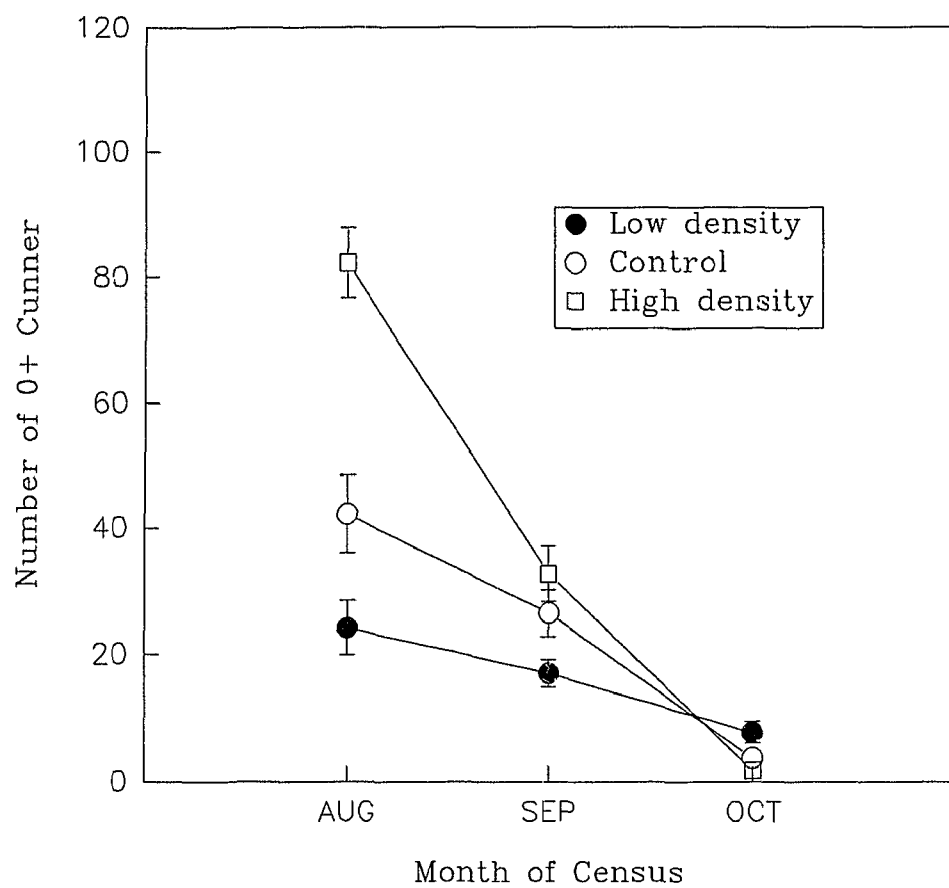


Fig. 3.5

Fig. 3.6 Effects of conspecific recruit density on (a) post-settlement survival, and (b) growth rate of 0+ cunner. Low density: recruit density artificially reduced to 3 m⁻²; Control: recruit density unmanipulated; High density: recruit density artificially increased to 10 m⁻². Vertical error bars represent ± 1 standard deviation.

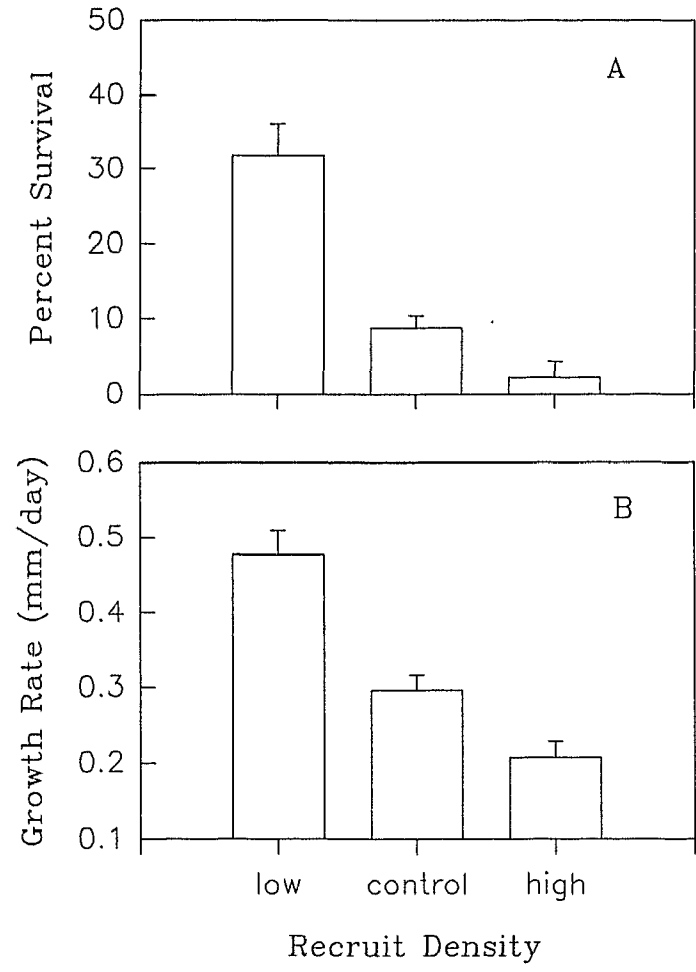


Fig. 3.6

DISCUSSION

Adult conspecific density had no effect on settlement of age 0+ cunner (Fig. 3.2a). Previous studies of the effects of adults on settlement on conspecifics have demonstrated a range of results, i.e. facilitation of settlement (Sweatman 1985, 1988), no effect (Sweatman 1985; Jones 1987; Levin 1993), or inhibition of settlement by adults (Shulman 1984, 1985a; Tupper and Hunte 1994). Several explanations for these respective results have been offered. Sweatman (1988) demonstrated experimentally that settling larvae of the pomacentrid Dascyllus aruanus were attracted by chemical cues to reefs occupied by conspecifics. Tupper and Hunte (1994) found that high densities of adult conspecifics inhibited settlement of 2 labrids (Thalassoma bifasciatum and Halichoeres garnoti) and a pomacentrid (Stegastes partitus) on some reefs, while on other reefs, adult density had no effect on settlement of conspecifics. Shulman (1984, 1985a) also observed that adult beaugregory (Stegastes leucostictus) directly inhibited settlement of 3 other species by chasing and/or eating the settling fishes. In this study, however, newly settled cunner (i.e. < 1 week post-settlement) were not observed to compete with adults, nor with each other. However, growth of juvenile cunner during the first few weeks post-settlement is rapid, and after 7-10 days, juvenile cunner begin occupying individual shelter sites, for which they compete with older residents (unpublished observations). Thus, the density-dependent effects of adult cunner on juvenile conspecifics may not begin until a week or more after settlement.

Post-settlement survival and recruitment strength of cunner were enhanced by removal

of resident conspecifics (Figs. 3.2b, 3.5a). Elevation of adult density to approximately twice natural levels resulted in 100% postsettlement mortality, while removal of conspecifics resulted in enhanced recruitment success over natural populations. This indicates that natural adult population density on the boulder reefs is sufficiently high to result in density-dependent post-settlement mortality and density-dependent recruitment, as has been recently demonstrated for a number of reef fish species (Stimson 1990; Hunt von Herbing and Hunte 1991; Tupper and Hunte 1994). In areas of patchy adult distribution, density-dependent mortality may modify patterns of density-independent settlement, such that the pattern of settlement is no longer reflected in the adult population (Connell and Jones 1991; Levin 1993, 1994a). Levin (1993, 1994a) reported post-settlement mortality of Gulf of Maine cunner inhabiting small artificial reefs to be greater than 99%, but the mortality was not density-dependent. The possible role of artificial habitat in this extreme mortality is unknown.

As population density increases, the available shelter per individual will decrease proportionately. The primary cause of density-dependent post-settlement mortality is most likely increased predation pressure on individuals that are unsuccessful in obtaining limited shelter sites (Hixon 1991; Hixon and Beets 1993). Habitats offering greater topographical complexity (i.e. more shelter sites per unit planar surface area) may buffer the effects of increased population density. In contrast, fish in low-complexity habitats may suffer density-dependent mortality at a lower threshold density. Thus, based on their physical structure, habitats may have differing carrying capacities above which density-dependent mortality occurs. The effects of habitat on recruitment success of cunner will

be dealt with in the following chapter.

Growth rate of 0+ cunner was depressed by high densities of resident conspecifics (Figs. 3.2c, 3.6b). This result was predicted from energetic budgets derived in Chapter 2, which showed that at high densities, cunner allocated a great deal more time and energy to shelter site defense, while foraging decreased (Table 2.5). Thus cunner at high densities are faced with the dual problem of extreme energy expense in defending shelter sites, compounded by a decrease in food intake. Removal of resident juveniles and adults both resulted in elevated growth rates of newly settled cunner, suggesting that natural adult population density on the boulder reefs is sufficiently high to depress growth of juvenile cunner. Density-dependent growth has been demonstrated for several species of coral reef fish (Forrester 1990; Jones 1990), as well as for at least one species of temperate demersal fish (Tupper and Boutilier 1994). The best evidence for density-dependent growth has been provided by studies of competition for limited food (Thresher 1983; Jones 1987a; Forrester 1990). Density-dependent growth may influence adult population size both directly and indirectly. First, since maturation and fecundity are generally more dependent on size than age (Jones 1991), the reproductive output of a population can vary as a direct consequence of growth. Second, many piscivores demonstrate size-selective predation concentrating on smaller size classes (Juanes 1994) and, as demonstrated in this study (Fig. 3.4), slower-growing individuals may be subject to higher age-specific mortality rates. Thus, density-dependent growth may be an important process leading to recruitment variation of demersal fishes.

Size at settlement was a good predictor of growth rate of juvenile cunner. Newly

settled cunner apparently establish size-dependent social dominance hierarchies soon after settlement, a result that has also been demonstrated for young-of-year cod (Gadus morhua) in St. Margarets' Bay (Tupper and Boutilier 1994), and for Dascyllus aruanus on the Great Barrier Reef (Forrester 1990). Since post-settlement mortality of cunner is size-dependent, with smaller individuals suffering higher mortality, large size at settlement confers an obvious advantage to juvenile cunner. The formation of such size hierarchies may be explained by asymmetric competition for food or by direct inhibition of growth through dominance interactions, which reduce surplus energy available for growth (Forrester 1990; Wootton 1990; Table 2.5).

In conclusion, density-dependent mortality and growth depression may arise from energy deficits caused by increased activity rates (e.g. Li and Brocksen 1977; Boisclair and Leggett 1989b; Chapter 2) and consequent reduced foraging rates (Table 2.5). This is particularly true in the case of species such as cunner, which engage in extremely expensive territorial or shelter site defense. These density-dependent effects may decouple patterns of recruitment success from patterns of larval settlement when conspecific density is high. At low population densities, recruitment may be more closely linked to settlement rate (i.e. larval survival). The results of this study support the emerging multifactorial view of recruitment dynamics (Jones 1990, 1991; Hunte von Herbing and Hunte 1991; Levin 1993, 1994a,b; Tupper and Hunte 1994) and show that energy can play an important role in post-settlement processes and eventual recruitment determination.

CHAPTER 4

EFFECTS OF HABITAT ON SETTLEMENT, GROWTH AND POST- SETTLEMENT MORTALITY OF A TEMPERATE REEF FISH

INTRODUCTION

Reef fishes exhibit a bipartite life cycle with a pelagic larval phase followed by a relatively sedentary adult phase (Sale 1991). During the pelagic phase, widespread dispersal and severe mortality of larvae serve to decouple local settlement of larvae into the adult habitat from the reproductive activity of the resident population (Forrester 1990). Over the past 15 years, a number of competing models on the processes regulating structure and abundance of reef fishes have been debated. Early research suggested that larvae were overabundant and that competition for limited space resulted in density-dependent recruitment and/or post-recruitment mortality. Populations of reef fish were therefore expected to remain in equilibrium at or near a carrying capacity, or maximum sustainable abundance (Smith and Tyler 1972; Sale 1977, 1978). This was known as the "space-limitation model". Later studies focused on the stochastic survival of reef fish larvae and suggested that adult population density was limited by larval supply (Doherty 1982, 1983; Victor 1983, 1986). This "recruitment-limitation" model

argued that recruitment was independent of resident density and that density-dependent competitive interactions had little importance in determining adult population size. Populations of reef fish were therefore nonequilibrium, and variation in adult abundance reflected variation in the magnitude of settlement.

Until recently, these models have been viewed by the majority of reef fish ecologists as mutually exclusive (Doherty and Williams 1988). However, a growing number of studies have demonstrated intraspecific variability in the determination of adult population size by processes occurring pre- or post-settlement. For example, Victor (1983, 1986) reported that populations of Thalassoma bifasciatum in Caribbean Panama were limited by larval supply, while Hunt von Herbing and Hunte (1991) and Tupper and Hunte (1994) found that populations of T. bifasciatum in Barbados displayed density-dependent post-settlement mortality and in some cases, density-dependent settlement. The primary focus of current research is on assessing the relative importance of settlement and postsettlement processes and identifying which processes have the greatest potential to modify patterns of settlement (Shulman and Ogden 1987; Forrester 1990; Jones 1990, 1991; Connell and Jones 1991; Hunt von Herbing and Hunte 1991; Levin 1993, 1994a,b; Doherty and Fowler 1994; Tupper and Hunte 1994).

Mortality, movement and growth are the most commonly studied post-settlement processes; all are capable of substantially modifying patterns of settlement and strongly influencing recruitment success (Jones 1990; Connell and Jones 1991; Jones 1991). Although early post-settlement mortality of reef fishes is known to be high (Shulman and Ogden 1987; Sale and Ferrell 1988; Connell and Jones 1991; Levin 1993, 1994a), the

magnitude and variability of mortality, relative to settlement, is unknown for most species (Connell and Jones 1991), as is the mechanism behind this mortality. In general, mortality of newly settled fish is attributed to predation (Houde 1987). Indeed, Hixon (1991) and Hixon and Beets (1989, 1993) suggest predation as a major factor structuring populations and communities of reef fishes. While several correlative studies (e.g. Shulman 1984) have found negative relationships between predator abundance and prey fish abundance, to our knowledge none have attempted to measure predation directly (see Hixon 1991).

Movement (emigration and immigration) has not been considered a major factor in the population dynamics of reef fish, due to their strong site fidelity (Doherty 1983; Aldenhoven 1986; Connell and Jones 1991; but see Forrester 1990). Growth, however, has received increasing attention as a factor critically important to the demography of juvenile and adult fishes (Jones 1986, 1987a, 1990; Forrester 1990; Connell and Jones 1991; Sogard 1992). Growth may influence adult population size directly, by controlling the number of individuals reaching reproductive maturity (Jones 1987a, 1991), or indirectly, through the effects of size-selective mortality on juvenile survival (Forrester 1990; Sogard 1992). Rapid growth means less time spent in the smaller, potentially more vulnerable size classes (Post and Evans 1989a). In temperate reef fishes, rapid growth may confer an additional, physiological advantage, since overwinter survival is generally higher in larger individuals (Henderson et al. 1988). Growth of juvenile fishes can be limited by food supply (Jones 1986, 1987a; Forrester 1990; Sogard 1992) or regulated by hierarchical social inhibition (Forrester 1990; Tupper and Boutilier 1994).

Settlement and post-settlement demography of reef fishes may be affected by structural characteristics of the habitat (Connell and Jones 1991; Levin 1991, 1993, 1994a). Habitat structure has been implicated in the determination of settlement (Sale et al. 1984), post-settlement mortality (Shulman 1984; Behrents 1987; Sogard 1992; Levin 1993, 1994a), movement (Robertson 1988a,b) and growth (Jones 1986; Sogard 1992). Certainly, many studies have found the distribution and abundance of fishes to be correlated with the amount and type of available habitat (Shulman 1984; Connell and Jones 1991; Levin 1991, 1993; Sogard 1992). Characteristics of habitat that are known to influence population size include depth (Thresher 1983), reef size (Shulman 1984), reef isolation (Walsh 1985), vertical relief (Thresher 1983; Chandler et al. 1985), coral or vegetation cover (Bell and Galzin 1984; Levin 1991), and topographic complexity (Luckhurst and Luckhurst 1978; Chandler et al. 1985; Roberts and Ormond 1987, Connell and Jones 1991). Of these, topographic complexity exerts perhaps the greatest influence on post-settlement processes. A more complex habitat may offer more shelter, resulting in reduced predation pressure (Behrents 1987; Connell and Jones 1991; Levin 1991). Several studies have shown survivorship of newly settled fishes to be strongly influenced by the availability of refuge sites, particularly in the presence of predators and/or conspecifics (Shulman 1984; Behrents 1987; Hixon and Beets 1989; Connell and Jones 1991). Habitat complexity may also influence growth and survival through increased prey density and diversity (Holbrook and Schmitt 1988; Connell and Jones 1991; Sogard 1992).

While selection for microhabitat at settlement is well-documented (Jones 1984; Sale

et al. 1984; Eckert 1985; Breitburg 1989, 1991; Levin 1993), little is known about the importance of habitat structure to post-settlement processes. For most species it is unknown whether habitat structure determines patterns of settlement or subsequently modifies them, and whether post-settlement processes alter or reinforce patterns of settlement (Jones 1990). This study examines the influence of habitat on settlement, growth and post-settlement mortality of the temperate labrid, Tautogolabrus adspersus. I employed mark-recapture techniques to quantify movement and mortality of newly-settled fish, and to measure individual growth rates in situ. To determine the role of predation in determining post-settlement mortality, I measured predation efficiency in four different habitat types. I then attempted to relate patterns of early survivorship to patterns of growth and predation, and to determine the relative influence of settlement and post-settlement processes on the recruitment success (operationally defined as the density of 0+ fish surviving for an arbitrary period following settlement) of T. adspersus.

METHODS

Species and Study Sites

The cunner, Tautogolabrus adspersus, is a common nearshore species ranging from Conception Bay, Newfoundland, south to Delaware (Scott and Scott 1988). Cunner occur from the intertidal zone (Whoriskey 1983) to depths of nearly 100 m on offshore banks (Scott and Scott 1988). Along the Atlantic coast of Nova Scotia and in the Gulf of

Maine, cunner spawn mainly in late July and August; settlement occurs about 3 weeks later and is restricted to a period 2 to 4 weeks in length (Levin 1991, 1993, 1994a; Tupper unpubl.). After settlement, cunner remain tenaciously site-attached for the first 1-2 years of demersal life (Tupper unpubl.). Newly settled cunner appear to feed opportunistically on small benthic invertebrates; crustaceans (amphipods and isopods) are the preferred prey (Levin 1994b). Cunner are found in a wide variety of habitats, but are generally associated with structure, including macroalgae (Levin 1991), rocky reefs, wrecks and pilings (Scott and Scott 1988; Auster 1989). They are active by day, but enter a period of torpor at night (Olla et al. 1979). During this time they shelter under rocks, in crevices, or among vegetation (Dew 1976). If suitable shelter is not available, cunner will adopt a banded colour and lie in a torpid state on open bottom (personal observations). While the banded colour may offer some camouflage, dormant cunner on exposed bottom are still at much greater risk of predation than their sheltered counterparts.

The study was conducted in St. Margaret's Bay, Nova Scotia, and was replicated at 3 discrete sites. The nearshore bottom of St. Margaret's Bay can be divided into four broad habitat types: rocky reef (characterised by bedrock strewn with large granitic boulders), cobble bottom, seagrass (*Zostera marina*) beds, and sand bottom. All habitat types were represented equally at each of the 3 sites. At each site, 4 x 15 m replicate transect lines were laid in each of the four habitat types. All transects were within 100 m of shore, at a depth of 1.5 to 2 m (mean low tide). Settlement, resident densities, growth rates, and predation rates were assessed in reef, cobble, grass and sand habitats

at each site, using a 2-factor (3 sites by 4 habitats) experimental design (see Sogard 1992). The substrate rugosity (a measure of habitat complexity, see Chandler et al. 1985) of each transect site was estimated by fitting a fine-link brass chain to the bottom contours along the transect line. The total distance covered by the chain was then divided by 10 meters (the horizontal distance covered by the transect line), producing an index of substrate rugosity. It is important to note that substrate rugosity is simply a measure of the actual surface area of bottom structure available to an organism and does not account for other possible shelter sites, such as that provided by macroalgae or seagrasses. The association of newly settled fish with macroalgae has been well documented for cunner in the Gulf of Maine (Levin 1991, 1993, 1994a). However, at the sites in St. Margarets' Bay, intense grazing by sea urchins Strongylocentrotus drobachiensis has reduced algal cover on hard bottom to a short filamentous turf. Within seagrass beds, young-of-year cunner were always observed in association with hard bottom (scattered rocks, debris, empty scallop (Placopecten magellanicus) shells, etc.). This suggests that at these sites, vegetation is less important in providing shelter than the physical structure of the bottom per se.

Census techniques

Visual censuses of abundance were conducted at roughly ten-day intervals from July 1 to November 6, 1991, and from July 7 to November 9, 1992, by snorkelling slowly along the transect lines and counting all individuals within one meter on either side of the

transect line (20 m² planar surface area). During the recruitment season (mid-August to early September), newly settled cunner were collected daily from each transect. Cunner were captured using a 10% solution of anaesthetic (quinaldine sulfate (Sigma)) in seawater, measured to the nearest mm with a 100 mm plastic ruler, and marked with injections of acrylic paint, using a specific pattern of colours and dots to identify individuals. This allowed marked individuals to be recognized as prior residents in subsequent censuses, and allowed quantification of growth, mortality and movement at each site. Continuous records of water temperature were not available for the specific study sites, but were available from an aquaculture site at the head of St. Margaret's Bay, approximately 2 km from the study sites. Water temperatures on each transect were recorded immediately following a census with a mercury thermometer held at the sediment-water interface.

Predation

It would be impossible to directly measure the rate of predation and the proportion of mortality attributable to predation without 24-hr surveillance throughout the entire settlement and post-settlement period. Instead, I compared spatial patterns of predator density and predator success to spatial patterns of juvenile survivorship and post-recruitment density, to determine if post-recruitment demography could be explained by variation in predation. At each transect site, detailed observations of predation by other fishes on young-of-year cunner were made in situ. Observations were conducted during

the late afternoon, in late September of 1991 and 1992. The observer floated motionless above the site while recording the species and number of predators, the number of attempted strikes (lunges at a cunner), and the number of successful strikes (capture and ingestion of a cunner) over a one hour observation period. An index of predator success was then calculated by dividing the number of successful strikes by the total number of strikes, for each of the four habitat types. Mean predator success in each habitat was calculated as the average predator success over the 12 transects (4 transects per habitat at each of 3 sites)

Data Analysis

Adult density, settlement, juvenile survivorship, recruitment success (density of 0+ cunner remaining in November, approximately 8 weeks after the end of the settlement season), and growth rate were compared among sites, habitats and years using 3-way analysis of variance (Sokal and Rohlf 1981). All numeric data were tested for homogeneity of variance using Bartlett's Test, and $\log(x+1)$ transformed where necessary to ensure homoscedasticity (Wilkinson 1990). Predator densities and success rates were also compared among sites, habitats and years using 3-way analysis of variance. In order to determine where significant differences among sites or habitats occurred, post-hoc analyses were conducted using Tukey's HSD (Wilkinson 1990). Linear regression analyses were used to determine the effects of substrate rugosity on settlement, post-settlement survival, predator success, growth rate and post-recruitment density.

RESULTS

Variation in environmental parameters

On any day throughout the study, there was less than 1 Celsius degree difference in temperature between locations and between transect sites at a location. It was therefore assumed that differences in growth between habitats or locations were not attributable to spatial variations in temperature. The general uniformity of temperature across the lower reaches of St. Margaret's Bay is most likely due to regular tidal flushing.

Mean substrate rugosity (measured for each habitat type as the average of the 12 transects) differed significantly between all of the four habitat types (ANOVA, $F = 12.37$, $p < 0.05$; Tukeys' HSD, $p < 0.05$ for all pairwise comparisons). We are therefore confident that the four habitat types chosen represent real differences in terms of the amount of shelter available to newly settled cunner.

Adult Distribution and Abundance

Population density of adult cunner varied greatly between habitats (ANOVA, $F = 613.5$, $p < 0.001$), although within a given habitat temporal variation in adult density was low ($F = 0.057$, $p > 0.05$). A significant site-by-habitat interaction ($F = 8.7$, $p < 0.001$) resulted from a high density of adults in the seagrass bed at the Birch Head site. Adult cunner were absent from sand bottom in all censuses. In both 1991 and 1992, mean adult

Fig. 4.1 Among-habitat variation in mean population density of adult cunner at 3 sites in St. Margarets' Bay, Nova Scotia. Data are from censuses conducted at 10-day intervals from August to November, 1991 and 1992. Vertical error bars represent ± 1 standard deviation.

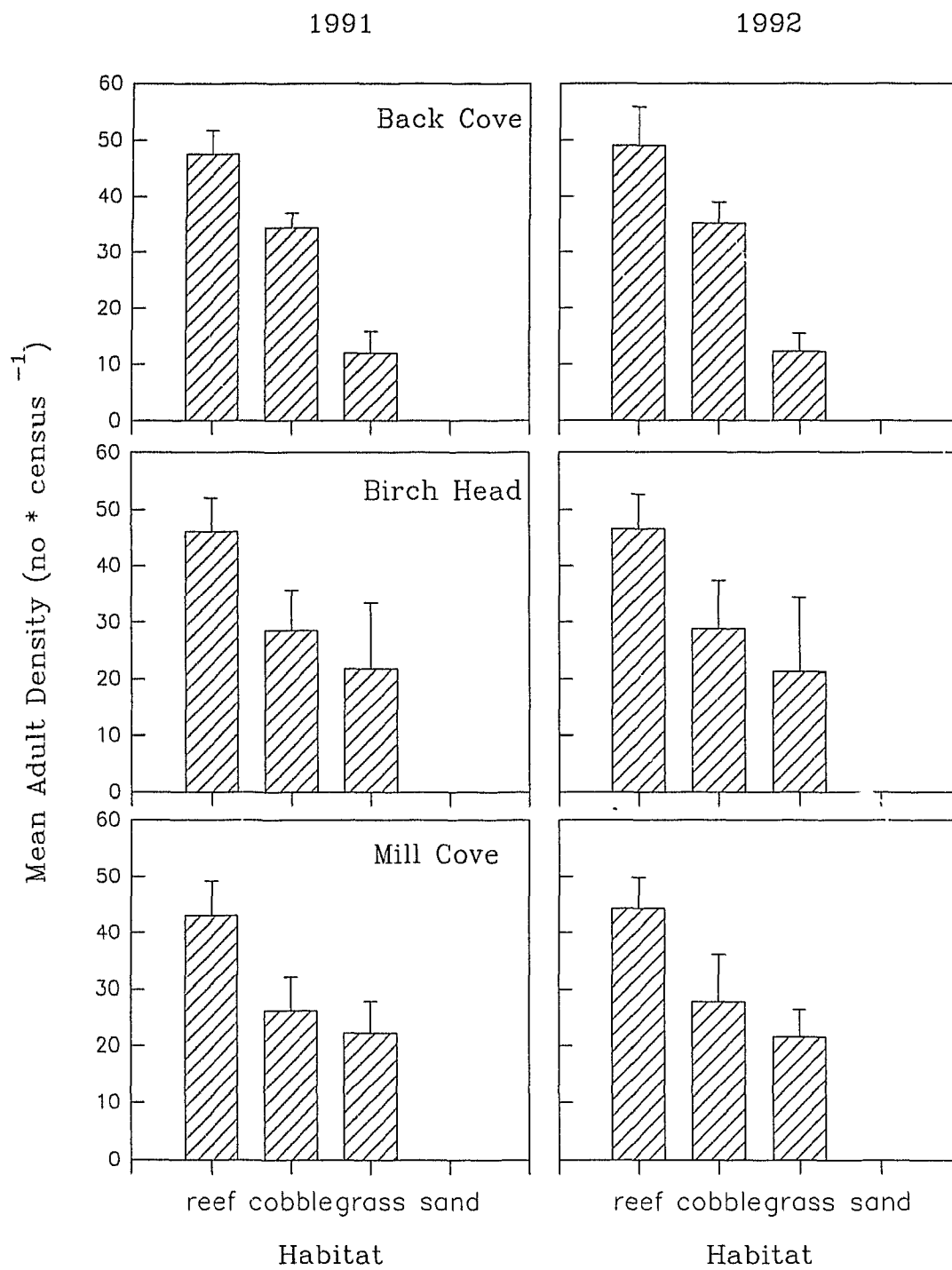


Fig. 4.1

density was positively correlated with substrate rugosity ($r^2 = 0.65$, $p < 0.001$ and $r^2 = 0.87$, $p < 0.001$, respectively; Fig. 4.2).

Settlement

No significant differences in settlement strength were found between habitat types, sites, or years (3-way ANOVA, $F < 0.70$, $p > 0.05$ for all variables; Fig. 4.3). Regression analyses showed no significant relationship between settlement of cunner and substrate rugosity of the transect sites ($r^2 = 0.0$, $p > 0.4$ for 1991; $r^2 = 0.0$, $p > 0.9$ for 1992). This suggests that cunner do not actively select microhabitats at settlement. In addition, mean settlement among habitats was not related to mean adult density in either year (Spearman's Rank Correlation, $r_s = 0.09$, $p > 0.8$ for 1991; $r_s = 0.06$, $p > 0.8$ for 1992), suggesting that the presence of conspecifics neither inhibited nor facilitated settlement of this species.

Juvenile survivorship and recruitment success

In 1991, the population density of age 0+ cunner rose rapidly at all transect sites following settlement in late August, then began to decrease in September (Fig. 4.4a). A similar pattern occurred in 1992 (Fig. 4.4b). The decline in population density was attributed to post-settlement mortality rather than emigration, since unmarked 0+ cunner were never observed on the transects, and occasional monitoring of the areas surrounding

Fig. 4.2 Effects of substrate rugosity on mean population density of adult cunner in St. Margarets' Bay, Nova Scotia. Data are from censuses conducted at 10-day intervals from August to November, 1991 and 1992.

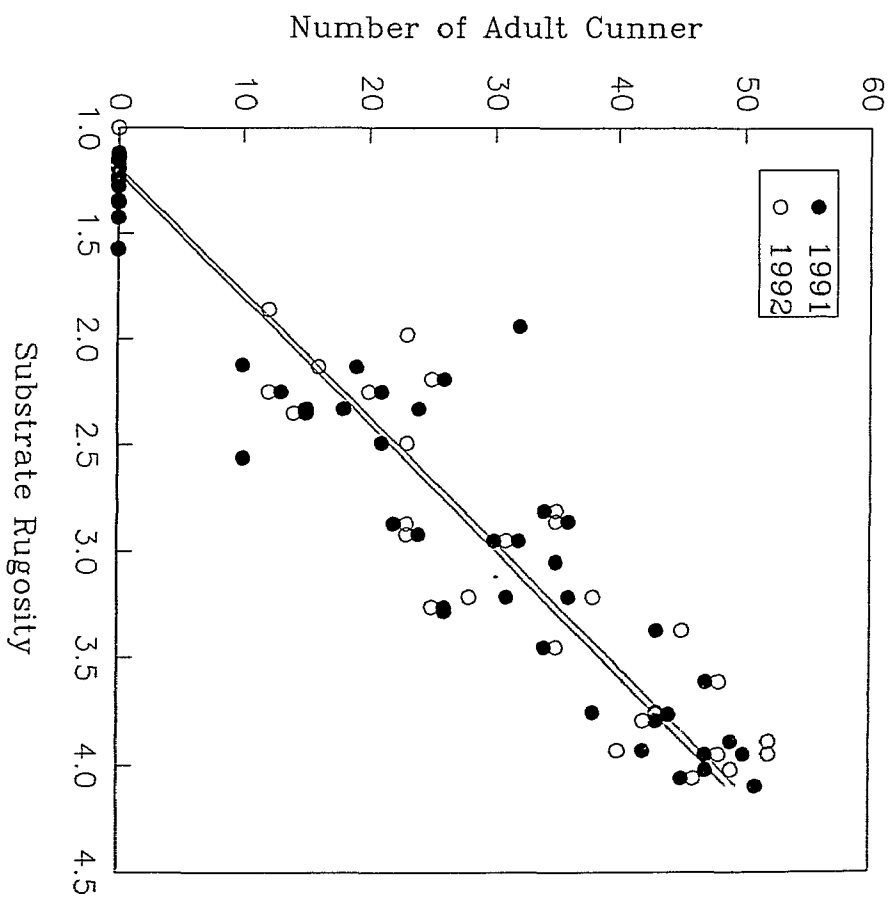


Fig. 4.2

Fig. 4.3 Among-habitat variation in settlement of cunner at 3 sites in St. Margarets' Bay, Nova Scotia, in 1991 and 1992. Vertical error bars represent ± 1 standard deviation.

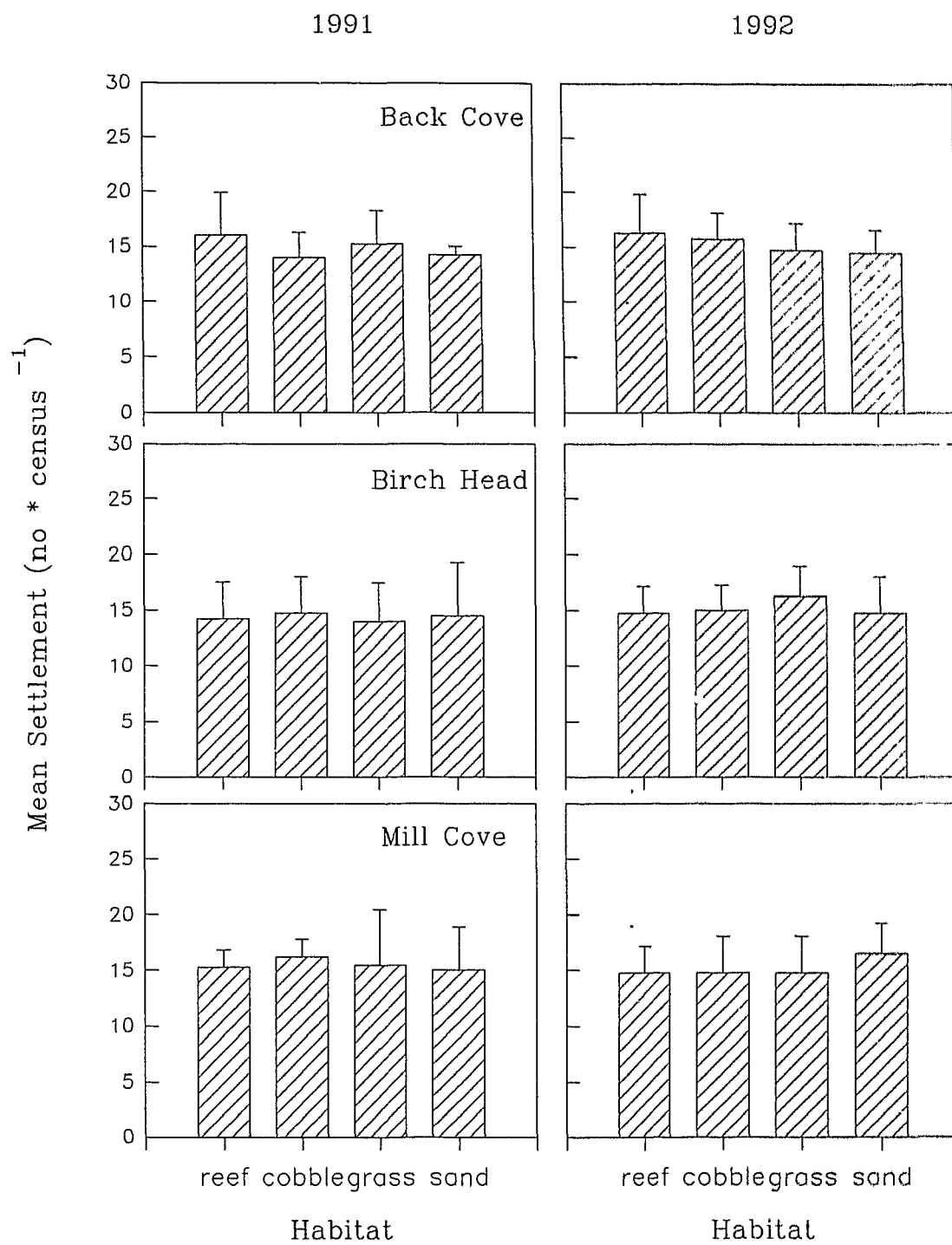


Fig. 4.3

Fig. 4.4 Temporal variation in population density of resident 0+ in cunner at 3 sites in St. Margarets' Bay, Nova Scotia, in 1991 and 1992, from censuses at 10-day intervals. Vertical error bars represent ± 1 standard deviation.

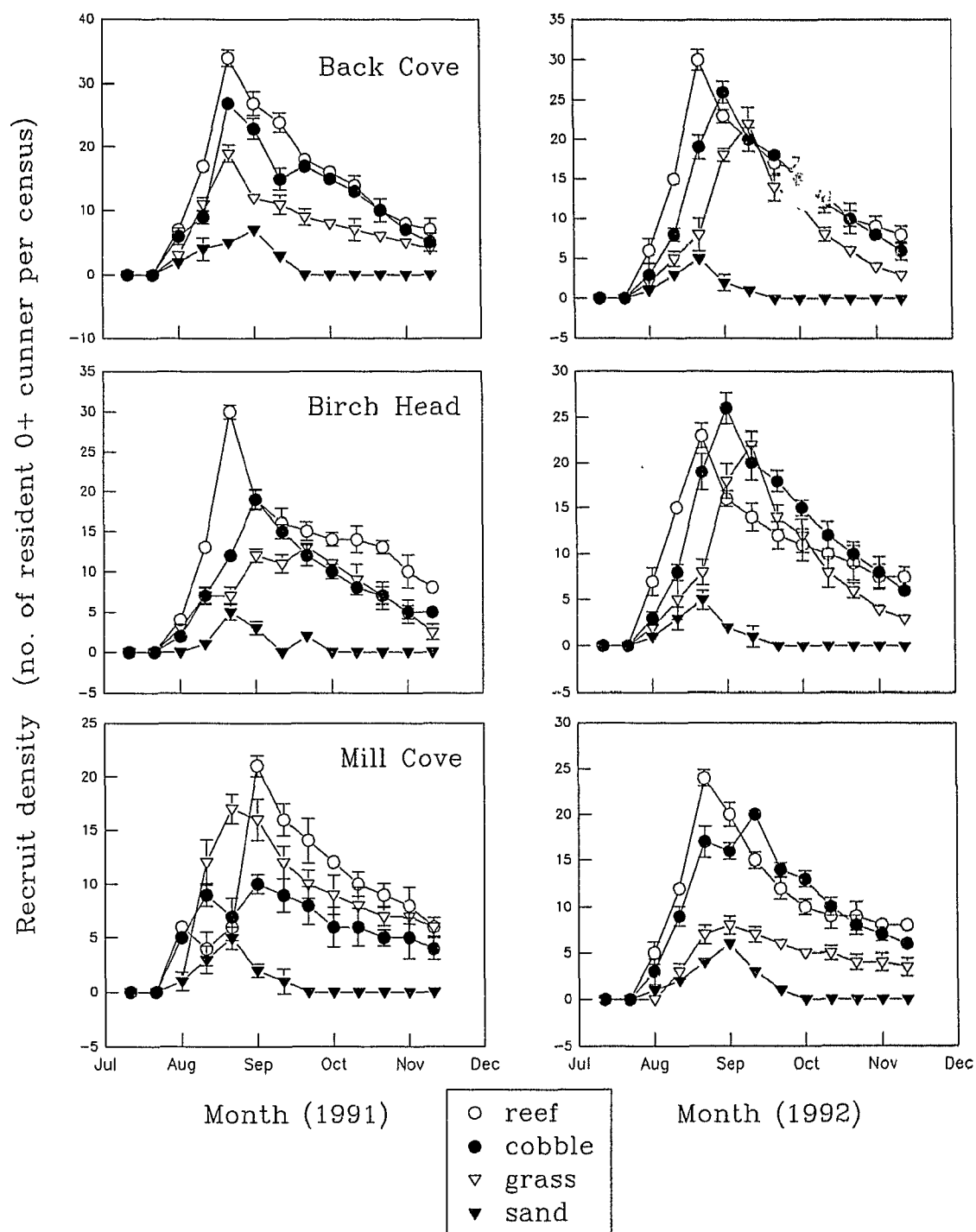


Fig. 4.4

the transects did not reveal the presence of any marked individuals. Survival of newly settled cunner varied widely among habitats (ANOVA, $F = 470.99$, $p < 0.001$; Fig. 4.5) but did not differ between sites ($F = 0.356$, $p > 0.05$). In most habitats, survival was significantly higher in 1992 than in 1991 ($F = 95.38$, $p < 0.001$; Fig. 4.5). Survival of newly settled cunner increased with increasing substrate rugosity (Fig. 4.6a) in 1991 ($r^2 = 0.68$, $p < 0.001$) and in 1992 ($r^2 = 0.59$, $p < 0.01$).

Among-habitat comparisons of mean post-recruitment population density (number of 0+ cunner remaining in November) revealed significant differences between habitat types (ANOVA, $F = 444.23$, $p < 0.05$). In pairwise multiple comparisons of habitat types, only reef and cobble habitats showed no significant difference in population density (Tukey's HSD, $p < 0.05$ for all pairwise comparisons except reef vs cobble). At all sites, density was highest on rocky reefs, followed by cobble, seagrass beds and sand (Fig. 4.7). This pattern suggests that Zostera blades are not suitable refuges for newly settled cunner. Within a given habitat type, density did not differ between sites. Juvenile density was significantly higher in 1992 than 1991 in most habitats and at all sites.

Regression analysis revealed a strong, positive relationship between the substrate rugosity of a transect site and the final post-settlement density of 0+ cunner (Fig. 4.6b); in 1991 ($r^2 = 0.91$, $p < 0.001$) and in 1992 ($r^2 = 0.90$, $p < 0.001$). In summary, despite a uniform pattern of settlement among habitats and sites, post-recruitment population density varied significantly between habitats and was positively correlated with the complexity of the habitat. These results suggest that juvenile cunner in St. Margaret's Bay are limited by the availability of shelter sites, and that suitable nursery habitats for

Fig. 4.5 Among-habitat variation in percent post-settlement survival of 0+ cunner at 3 sites in St. Margarets' Bay, Nova Scotia, in 1991 and 1992. Survival was calculated as number of 0+ cunner remaining on a given transect in November, divided by the total number of cunner to settle on that transect. Vertical error bars represent ± 1 standard deviation.

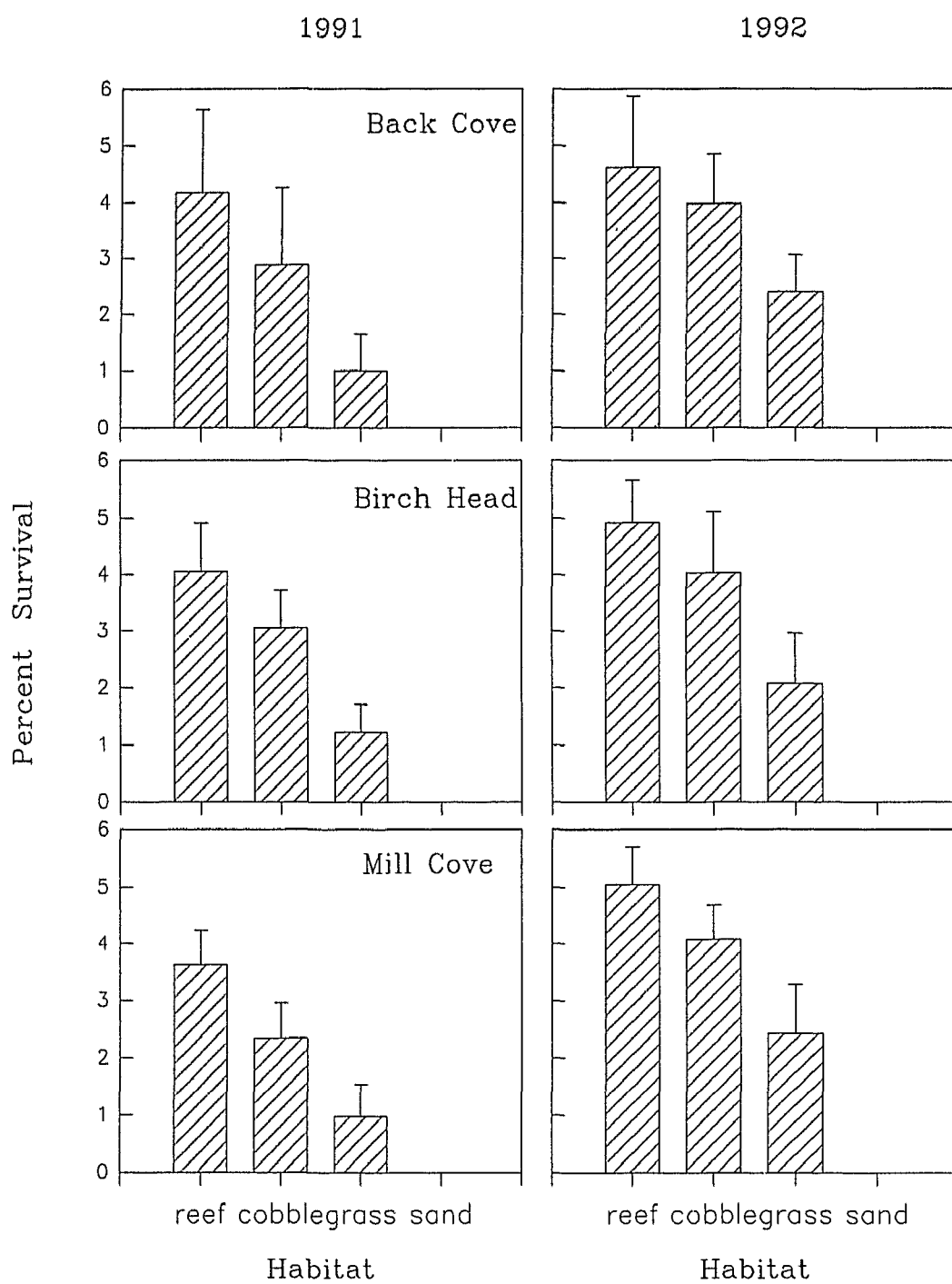


Fig. 4.5

Fig. 4.6 Effects of substrate rugosity on (a) post-settlement survival and (b) post-recruitment density of 0+ cunner in St. Margarets' Bay, Nova Scotia, in 1991 and 1992.

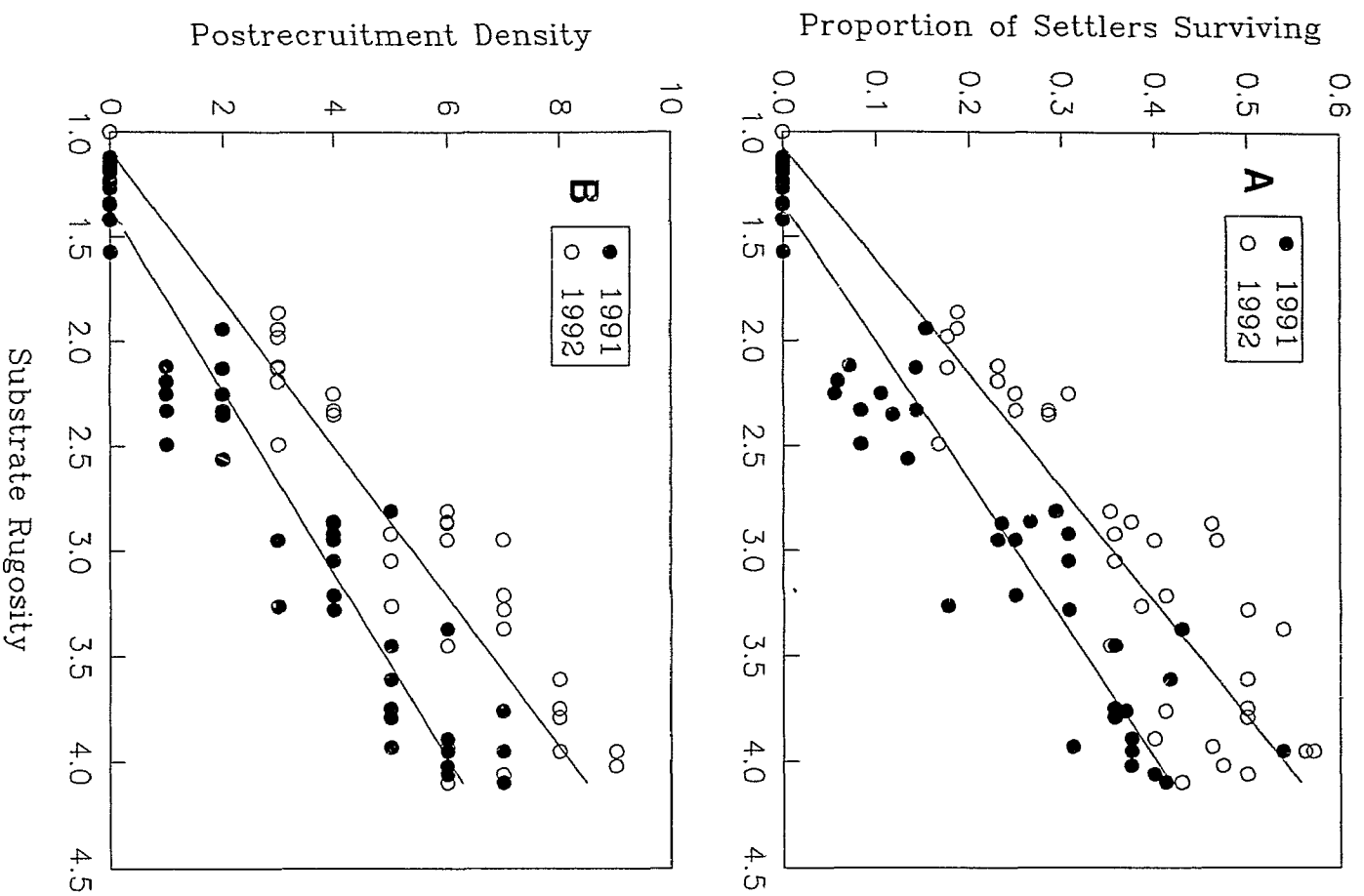


Fig. 4.6

Fig. 4.7 Among-habitat variation in post-recruitment density of 0+ cunner at 3 sites in St. Margarets' Bay, Nova Scotia, in 1991 and 1992. Vertical error bars represent ± 1 standard deviation.

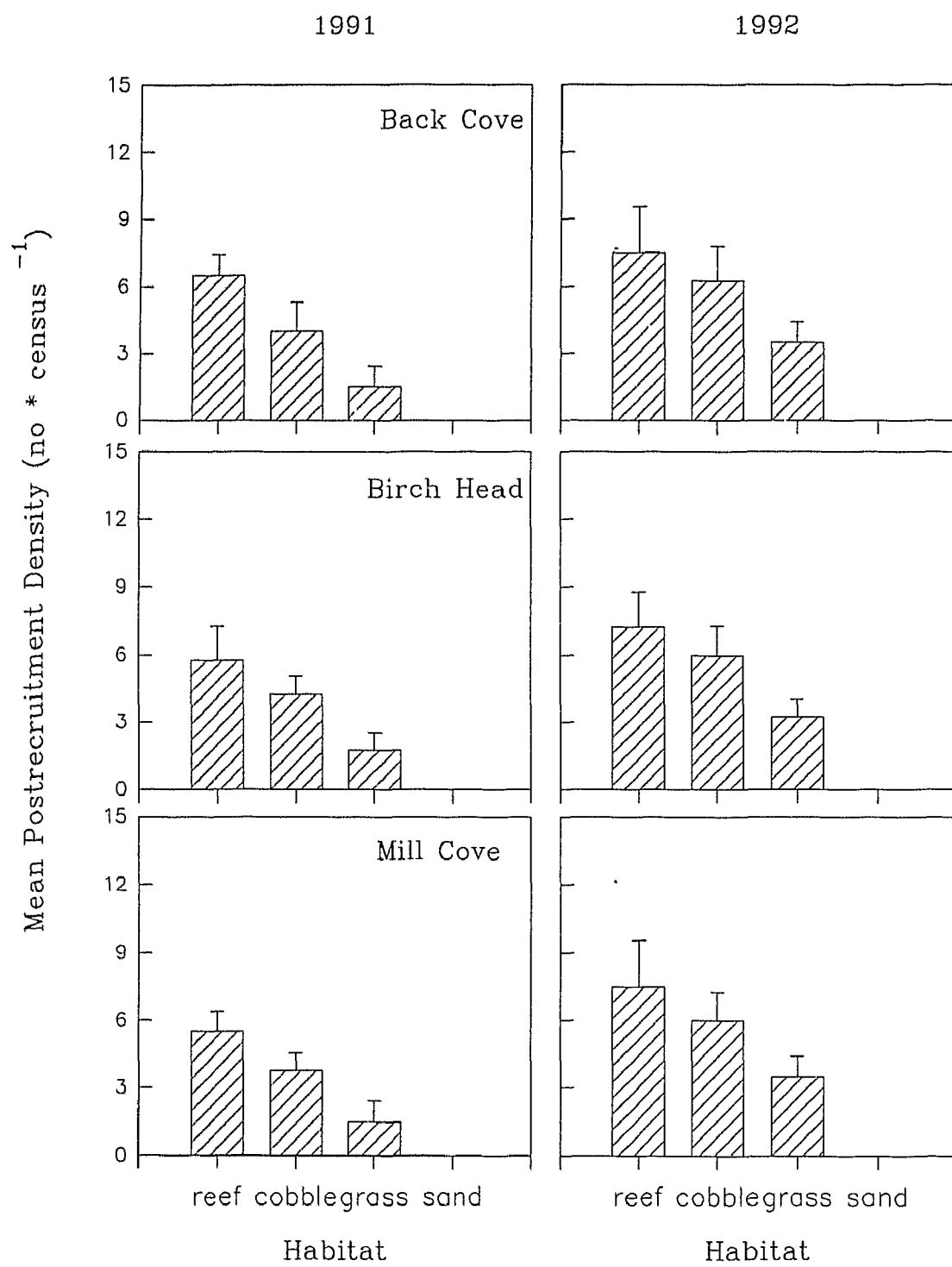


Fig. 4.7

juvenile cunner should provide an abundance of refugia.

The pattern of post-recruitment juvenile distribution was identical to the pattern of adult distribution. Mean post-recruitment density was positively correlated with mean adult density (Spearman's Rank Correlation, $r_s = 0.96$, $p < 0.001$ in 1991; $r_s = 0.90$, $p < 0.001$ in 1992); this has been suggested as evidence for facilitation of settlement or post-settlement survival by resident conspecifics (Sweatman 1985, 1988; Jones 1987; Forrester 1990). However, since substrate complexity, post-settlement survival, post-recruitment juvenile density and adult density were intercorrelated, it seems more likely that the correlation between juvenile and adult cunner simply reflects the greater suitability of complex substrates as cunner habitat (see also Connell and Jones 1991). Few large adult cunner (age 3+ or older) were present at the study sites. This may reflect a decrease in dependence of large cunner on the shelter offered by nearshore complex habitats (Pottle and Green 1979), presumably due to a decrease in their vulnerability to predation. Thus, while the presence of older, larger cunner may not point to a suitable habitat for cunner recruits (Levin 1993), the presence of age 1+ and 2+ fish may be a more reliable indicator.

Predation on juvenile cunner

Three species of the family Cottidae (Hemitripterus americanus, Myoxocephalus octodecemspinosus and Myoxocephalus aeneus) were observed preying on juvenile cunner during this study. Since these three species are confamilials with very similar behaviours,

they were pooled together as "cottid predators". Total density of cottid predators (1.7 cottids m⁻²) did not vary between habitats, sites or years (3-way ANOVA, $F < 1.50$, $p > 0.05$ for all variables). Capture success varied significantly among habitats ($F = 364.91$, $p < 0.001$), but did not differ between sites or years ($F = 2.11$, $p > 0.05$, and $F = 0.02$, $p > 0.05$, respectively). Predators were most efficient on open sand bottoms and least efficient in reef habitats (Fig. 4.8). Capture success was higher in seagrass beds than on reefs or cobble bottoms (Fig. 4.8), again suggesting that this type of vegetation does not provide optimal shelter for small cunner. Capture success was inversely related to substrate rugosity (Fig. 4.9), juvenile survivorship, and post-recruitment density in both years (Table 4.1). These results suggest that predation strongly influences juvenile survivorship and subsequent post-recruitment demographics of cunner.

Growth

A total of 83 marked recruits were recovered and remeasured in November 1991; 73 were recovered in November 1992. The extreme mortality suffered on sand bottom made it impossible to measure growth in this habitat. At all 3 sites, and in both years, growth rate of newly settled cunner was highest in seagrass beds (Fig. 4.10); this difference was significant (ANOVA, $F = 101.17$, $p < 0.001$). Growth rates on reef and cobble bottoms were not significantly different (Tukeys' HSD, $p < 0.05$). Growth rates in any habitat did not vary significantly between sites or years ($F = 0.713$, $p > 0.05$, and $F = 0.38$, $p > 0.05$, respectively). Growth was not related to habitat complexity in 1991 ($r^2 = 0.0$, $p > 0.75$)

Fig. 4.8 Among-habitat variation in capture success of cottid predators feeding on 0+ cunner in St. Margarets' Bay, Nova Scotia, in 1991 and 1992. Data from all sites are pooled. Vertical error bars represent ± 1 standard deviation.

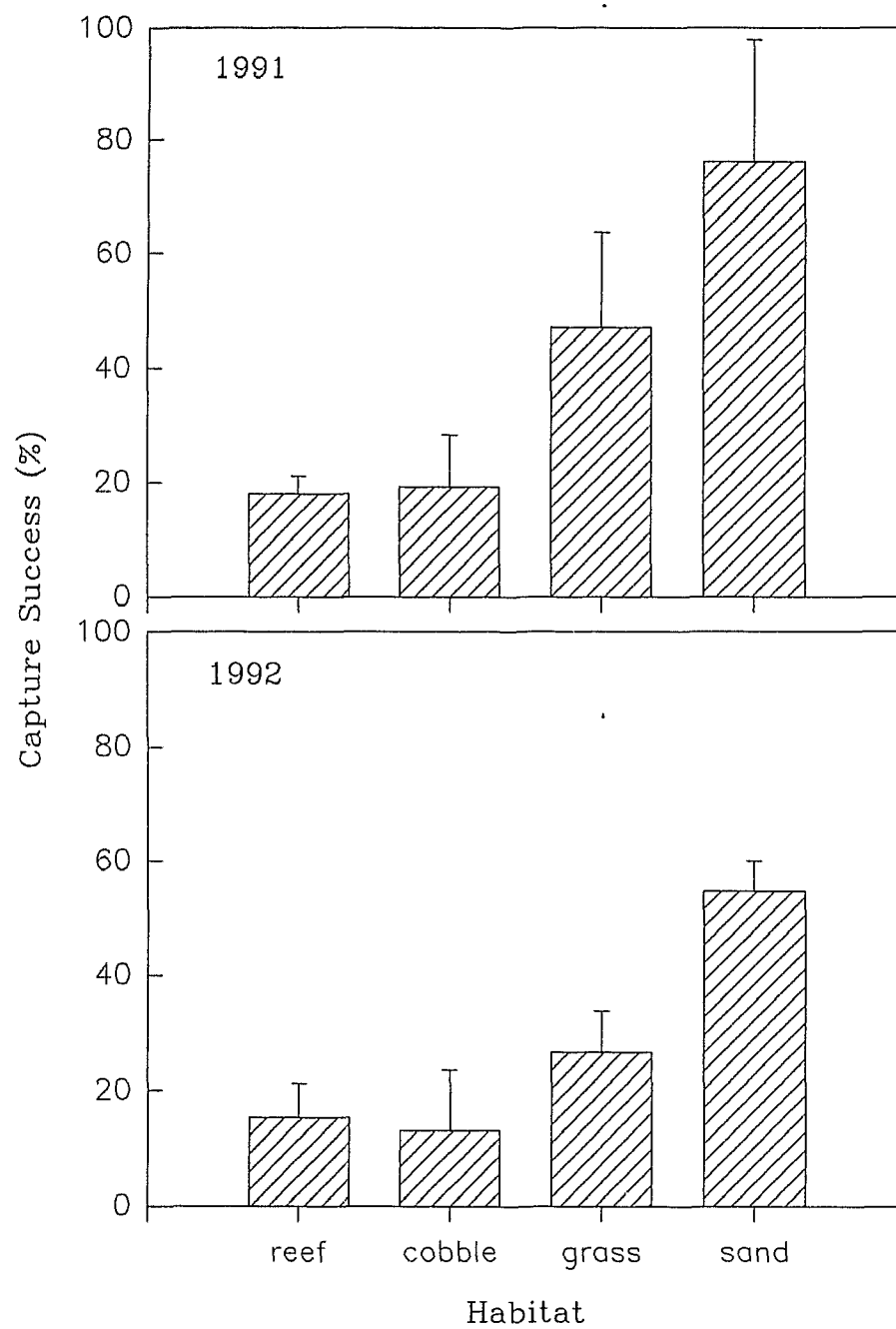


Fig. 4.8

Fig. 4.9 Effects of substrate rugosity on capture success of cottid predators feeding on 0+ cunner in St. Margarets' Bay, Nova Scotia, in 1991 and 1992.

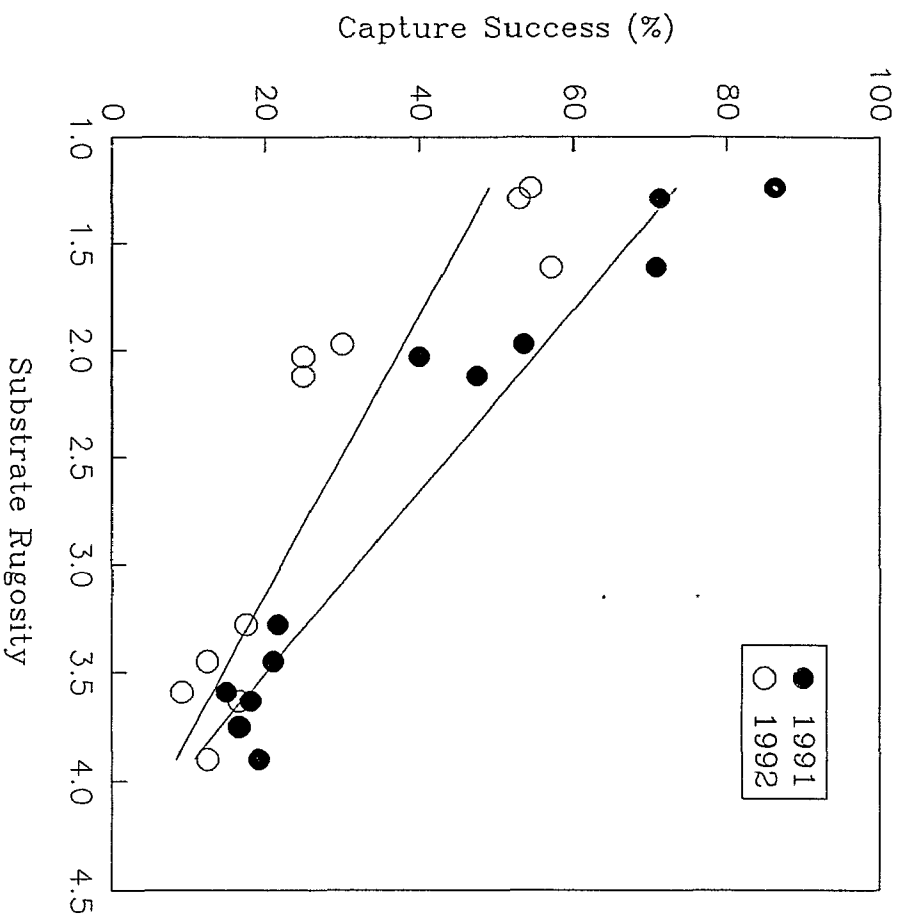


Fig. 4.9

Table 4.1. Regression of capture success on substrate rugosity, juvenile survival, and post-recruitment density (recruitment success) in 1991 and 1992.

Capture Success vs.	Year	r^2	p
substrate rugosity	1991	0.86	<0.001
	1992	0.88	<0.001
juvenile survival	1991	0.92	<0.001
	1992	0.81	<0.001
post-recruitment density	1991	0.92	<0.001
	1992	0.83	<0.001

Fig. 4.10 Among-habitat variation in growth rate of 0+ cunner at 3 sites in St. Margarets' Bay, Nova Scotia, in 1991 and 1992. Vertical error bars represent ± 1 standard deviation.

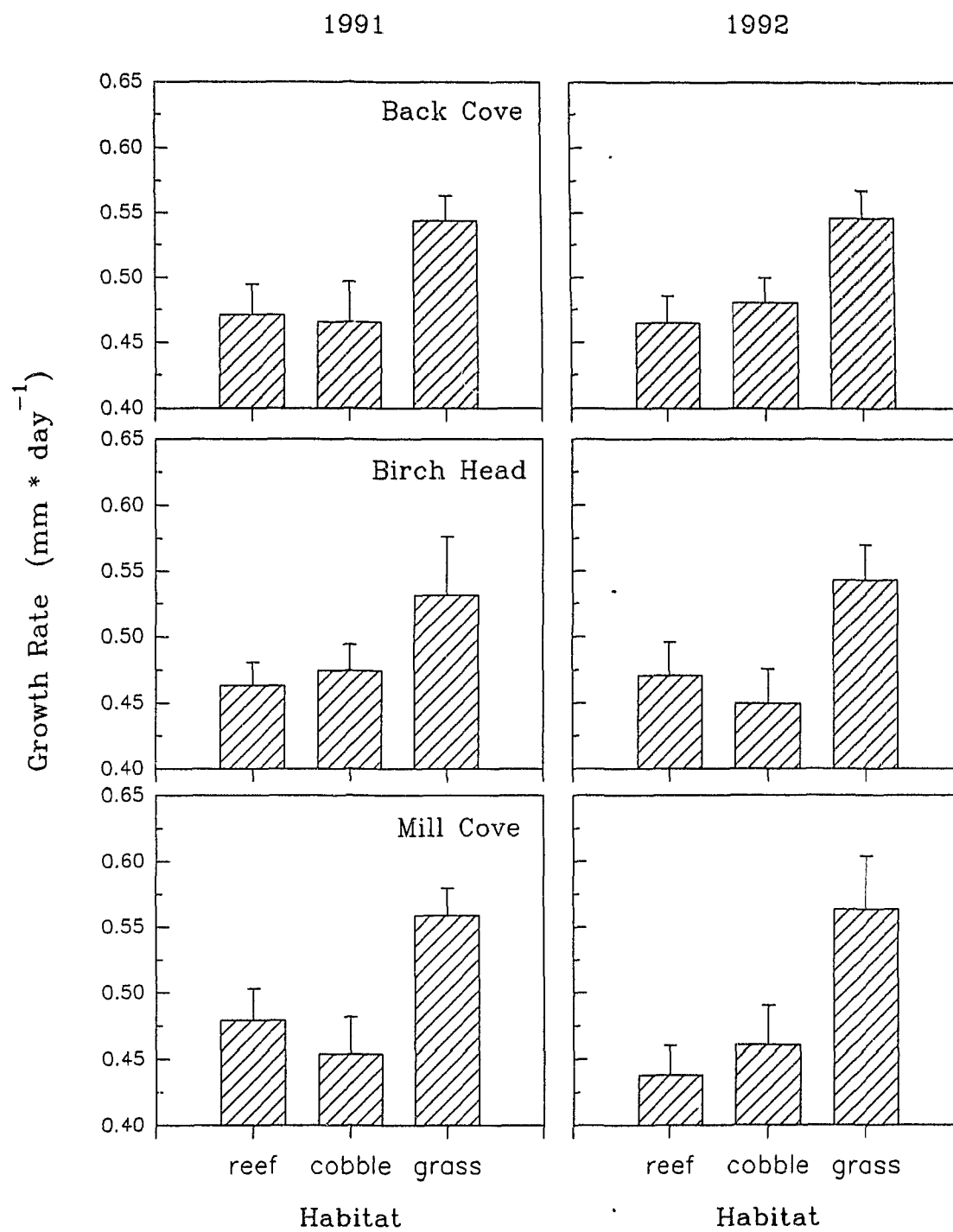


Fig. 4.10

or 1992 ($r^2 = 0.0$, $p > 0.70$), but may have been influenced by increased prey density in seagrass habitats (see Sogard 1992). The spatial pattern of variation in growth rate was unrelated to patterns of post-recruitment juvenile and adult densities, suggesting that population density had little effect on growth, at least at the levels encountered in this study. However, since population density in a given habitat did not differ among sites, I cannot comment on the effects of population density on growth in a particular habitat.

DISCUSSION

Relationship of Settlement to Population Size

Juvenile cunner demonstrated no preference for habitat type at settlement (Fig. 4.3). Moreover, the spatially uniform pattern of settlement was unrelated to the spatial pattern of post-recruitment juvenile (Fig. 4.7) or adult density (Fig. 4.1). In contrast to patterns of settlement, density of juvenile cunner 8 to 12 weeks after settlement varied greatly between habitat types (Fig. 4.7). The processes regulating among-habitat distributions of cunner must therefore occur post-settlement, with differential survival rather than differential settlement leading to the observed patterns of density.

The relative importance of settlement and post-settlement processes in determining fish-habitat associations is unknown for most species (Jones 1991). Sale et al. (1984) clearly demonstrated that several species of coral reef fish settle preferentially to specific microhabitats, and suggested that spatial variation in microhabitat structure may result in

spatial variation in settlement and subsequent recruitment. However, habitat type may influence post-settlement processes to either reinforce or alter spatial patterns established at settlement. For example, the damselfish Pomacentrus amboinensis settles preferentially in deeper lagoonal waters, where its subsequent growth rate and survival is higher than in shallow water (Jones 1986). In contrast, the blennoid fish Forsterygion varium settled uniformly among habitat types differing in structural complexity, but exhibited extreme differences in subsequent survival and density, both of which were much higher in more complex habitats (Connell and Jones 1991). The blennoid pattern of settlement and post-settlement survival is identical to that exhibited by juvenile cunner in this study. As with F. varium, among-habitat variation in the survival of juvenile cunner dramatically altered patterns of settlement. Levin (1994a) studied cunner on small artificial reefs in the Gulf of Maine, and also concluded that differential mortality "played an obvious and important role in determining the numbers of recruits at the end of the settlement season".

Influence of habitat structure and predation on juvenile demography

The existence of a positive correlation between the density of juvenile fish and habitat complexity has been considered evidence for space-limitation, i.e. intraspecific competition for limited shelter sites (e.g. Shulman 1984). In this study, predation efficiency of cottid predators decreased in more complex habitats (Fig. 4.5), and similar results were observed for predation on amphipods by yellow perch, Perca flavescens, and ruffe, Gymnocephalus cernuus (Mattila 1992). Gotcietas and Brown (1992) found that

young-of-year cod (Gadus morhua) kept in aquaria selected more complex substrates in the presence of a predator. Thus, the relationship between habitat complexity and population density need not be explained by competition for living space, but can instead be attributed to differential predation among habitat types. Although predation efficiency decreased in more complex habitats (Figs. 4.8, 4.9), a very high predator density in such habitats might still lead to higher predation mortality. In St. Margarets' Bay, predator density did not differ significantly between habitats. As a result, the total mortality attributed to predation remained inversely related to habitat complexity (Fig. 4.9).

Mattila (1992) suggests that predation efficiency is not automatically reduced by a high level of habitat complexity per se; the prey must be able to utilize that complexity as an effective shelter. In this study, seagrass beds could conceivably provide the greatest complexity of the 4 habitats if the vertical area of each blade of grass were measured. However, young-of-year cunner did not utilize seagrass blades as shelter - they preferred rocks, empty scallop shells, and other debris found within the seagrass beds. Considering the rapid post-settlement growth rates of young-of-year cunner, it seems likely that they essentially outgrow seagrass blades as a suitable refuge soon after settlement.

Connell and Jones (1991) hypothesized that the initial lack of variation among habitats in settlement of Forsterygion varium was due to the animals finding shelter in a wide range of habitats, whereas subsequent variation among habitats in post-settlement mortality may have arisen from newly settled fish outgrowing suitable shelter in low-complexity habitats. Our findings for cunner support this hypothesis. If cunner, at their smallest sizes (8-15 mm), can utilize all habitats more or less equally, variation in

settlement to different habitats would not be expected. Patterns of distribution of post-recruitment juvenile cunner would then be determined by habitat-specific predation pressure. This forms the basis for the "predation hypothesis" (Hixon 1991) which states that post-settlement mortality due to piscivory determines patterns of adult abundance. Lough et al. (1989) offered a similar hypothesis to explain the demography of young-of-year cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) on Georges Bank. They observed that pelagic juvenile gadids were widespread over the bank in June, but that in July, demersal juveniles were found mainly on pebble-gravel beds and were "poorly represented" on other, less complex sedimentary substrates. They also suggested that, in addition to providing more shelter sites than the other substrates, the pebble-gravel deposits most closely matched the mottled colouring of demersal juvenile cod, making the small fish very difficult to see, and therefore reducing their predation risk. From these results, Lough et al. (1989) concluded that the availability of a complex habitat with reduced predation pressure may be critical to the recruitment success of cod and haddock on Georges Bank.

Growth

Cunner do not remain active over winter; once the water temperature reaches about 5°C, they become torpid and rest within refuge sites until the following spring (Dew 1976). Cunner are sexually mature at about 54-60 mm standard length, a size they usually reach as one-year-olds (Dew 1976), although Johansen (1925) reported that cunner

on the Scotian Shelf do not reach sexual maturity until age 2, due to the shorter growing season. However, the shallow nearshore waters of St. Margarets' Bay are notably warmer than Scotian Shelf waters, and age 1+ fish were often observed spawning at the study sites. Since cunner do not feed or grow over the winter months (Auster 1989), they must approach the size of sexual maturity by the start of their first winter in order to join the adult population the following summer. Moreover, many temperate marine fishes rely on stored lipids to survive the winter, and survival is higher in larger individuals (Henderson et al. 1988). Thus, post-settlement growth rate is crucial to the timely replenishment of adult populations, as well as to the lifetime fitness of individual cunner.

Growth rates of 0+ cunner in this study are in agreement with published values (Bigelow and Schroeder 1953); mean growth rate of all recaptured cunner was approximately 0.5 mm day^{-1} . Connell and Jones (1991) have suggested that habitat complexity may influence growth and survival of juvenile fish through increased prey density and prey diversity. Growth rate of young-of-year cunner differed between habitats (Fig. 4.10), but was not related to substrate rugosity *per se*. However, as discussed in the previous section, the shelter provided by Zostera blades was not accounted for by our measure of substrate rugosity. For small prey items, seagrass beds undoubtedly offer the greatest habitat complexity. Thus, if habitat complexity is measured relative to prey size rather than predator size, then prey densities and predator growth rates should increase with habitat complexity. For example, Sogard (1992) found that the presence of Zostera increased amphipod densities by 64% and copepod densities by 49%. She reported that growth rates of the tautog (Tautoga onitis), another temperate labrid, were higher in

vegetated habitats supporting higher prey densities. Tupper and Boutilier (unpubl. data) found that growth of 0+ Atlantic cod (Gadus morhua) in St. Margarets' Bay was higher in seagrass beds than on rocky reef, cobble or sand bottoms. They also attributed the higher growth rates to greater prey density in the seagrass habitat.

Several researchers have suggested the possibility of trade-offs in habitat utilization by fishes (Gilliam and Fraser 1987; Connell and Jones 1991; Sogard 1992; Levin 1993; Walters and Juanes 1994). Present ecological theory suggests that fish should select for the habitat that maximizes energy gain (growth), while minimizing the risk of mortality (Gilliam and Fraser 1987; Gotceitas 1990). In this study, 0+ cunner experienced elevated growth rates in seagrass habitats (Fig. 4.10), but experienced significantly reduced predation risk and mortality on reefs and cobble bottoms (Figs. 4.8, 4.5). It remains unclear which strategy offers the greater advantage for 0+ cunner. Cunner remain torpid without feeding over the winter months and rely on stored lipids to survive the winter (Dew 1976). Survival of cunner and other species in northern climates is generally correlated with body size, as larger individuals have larger lipid stores on which to draw (Shuter et al. 1985; Henderson et al. 1988). Tupper and Boutilier (unpubl. data) demonstrated a similar trade-off in the habitat selection of 0+ Atlantic cod (Gadus morhua). They suggested that in terms of replenishing the adult population, reef and cobble habitats might be viewed as supplying larger numbers of small individuals, each with a higher risk of mortality, while seagrass habitat might be viewed as supplying fewer numbers of large individuals, each with a higher chance of survival.

During the early juvenile phase, fish generally undergo a phase of fast growth in

which the proportion of absorbed food energy used for growth may reach 90% (Calow 1977). This study and others (Forrester (1990) and Tupper and Boutilier (unpubl. data)) have demonstrated that fast growth is important to juvenile fish in order to reduce the risk of size-selective predation. However, the high energetic cost of growth may substantially reduce the animals' scope for activity (the amount of aerobic energy available over and above maintenance requirements, see Fry 1947), thereby curtailing the performance of crucial activities such as predator avoidance, shelter site defence, etc. (Wieser 1989). Thus, a juvenile fish that is investing most of its metabolic energy in growth may be relatively inactive between bouts of feeding (Vahl and Davenport 1979). During hours of daylight, newly settled cunner spent roughly 32-59% percent of their time feeding and 36-62% inactive (usually in shelter), depending on habitat type (Table 2.2). The highest percentage of time spent in shelter sites was in reef and cobble habitats, where cunner suffered the lowest predation mortality. Following bouts of feeding, locomotory capacity is reduced by the energetic cost of digesting and absorbing food (apparent SDA; Jobling 1981). In juvenile cunner, feeding may reduce the scope for activity by as much as 60%, and the maximum swimming speed by up to 40% (Chapter 1). This may place the fish at a greater risk of predation, particularly if suitable shelter is not available at the time of highest SDA.

Conclusions and Implications for Models of Reef Fish Population Dynamics

The "space-limitation" hypothesis states that recruitment will depend on resident

conspecific density, either through direct inhibition of settlement, or through density-dependent post-settlement mortality (Shulman 1984, 1985a,b). Levin (1993, in press) found no measurable effects of conspecific density on settlement or subsequent recruitment success of cunner in the Gulf of Maine. However, investigation of the effects of resident density on settlement and post-settlement mortality requires an experimental approach in which adult density is manipulated within a set of replicate habitats. This approach was adopted in Chapter 3, the results of which demonstrate that although settlement was density-independent, post-settlement mortality and growth were strongly influenced by resident conspecific density.

The "recruitment-limitation" hypothesis states that variation in adult population density will directly reflect patterns of settlement. My results and those of Levin (1993, 1994a) indicate that patterns of settlement of cunner are modified by post-settlement mortality influenced by habitat structure, primarily through habitat-specific predation pressure. Considering the extreme mortality possible in the first week post-settlement (Shulman and Ogden 1987; Sale and Ferrell 1988; Levin 1994a; this study), this breakdown in the recruit-settler relationship can occur in a very short period of time.

The fact that settlement was independent of adult density does not necessarily mean that the availability of shelter is not limiting. In this study, post-recruitment juvenile density and adult density both increased with increasing habitat complexity. The "predation hypothesis" (Hixon 1991) argues that the presence of predators may induce competition for available refuge sites, and predation may thus limit population size, with the availability of shelter setting the maximum limit. Of all the alternative models

presented to date, the predation hypothesis best fits the available data for cunner (Levin 1993, 1994a; this study). However, any single-process model should be approached with caution as demographic processes may vary in relative importance with location, time and habitat (Jones 1990, Connell and Jones 1991). In this study, spatial patterns of settlement of cunner were dramatically altered by habitat-specific post-settlement mortality. However, in years or locations in which larval survival and settlement were very low, the importance of post-settlement processes would likely decrease, and the abundance of young-of-year cunner would be regulated mainly by larval input. Alternatively, a particularly cool summer could reduce growth rates to the point where fewer individuals reach sexual maturity, limiting the size of the breeding population and therefore reducing reproductive output. Longer-term studies are needed to assess the importance of pre- and post-settlement events over several years (Forrester 1990, Jones 1990), as are experimental studies involving the manipulation of conspecific densities, predator densities and habitat structure. In addition, energy can be considered a resource limiting the growth and survival of juvenile fish (Wieser 1989); further experimental studies should investigate the importance of energetics to the demographics of reef fish.

CHAPTER 5

INTRASPECIFIC VARIATION IN GROWTH AND METABOLIC EFFICIENCY OF CUNNER (Tautogolabrus adspersus)

INTRODUCTION

A central question in ecology is: what factors cause variation in the population abundance of animals? To understand why a population varies over time, the ecology of the individuals within that population must be understood (Lomnicki 1988). Since ecology is most often defined as the study of organisms in relation to their environment, a crucial approach is to determine the environmental factors that predictably influence the fitness (lifetime reproductive output) of individuals (Wootton 1990). Individuals are the units upon which natural selection operates and individuals within a population are not identical but show variation of structures, functions, or characters. Some of these variations result in the individual functioning more efficiently within its environment, i.e. becoming somewhat better adapted to its ecological niche (de Beer 1980 in Ware 1982). These individuals should survive longer and be more fecund, favouring their genetic representation in future generations (Ware 1982; Wootton 1990). Heritable traits that endow individuals with such a selective advantage might therefore be used as indicators

of differential fitness within a population. To date, the majority of research in the fields of ecology and physiology has been carried out at the population, species, or community level, rather than attempting to elucidate interactions between individuals and their environments (Arnold 1988; Lomnicki 1988).

As discussed in Chapter 2, individual organisms must allocate limited resources in a fashion that maximizes their genetic representation in future generations, i.e. in a way that optimizes the fitness of the individual (Sibly and Calow 1986; Wootton 1990). Energy can be considered a finite resource limiting the growth, survival and lifetime fitness of an individual. Ware (1982) suggests that surplus energy can be used as an interim measure of fitness. Intraspecific differences in metabolic efficiency, for example the energetic costs of feeding and locomotion, may result in differential survival of individuals, thereby transmitting the genes for efficient energy metabolism to future populations (Arnold 1988).

Aerobic metabolic scope (scope for activity) may be useful as an index of the potential fitness of individuals (Ware 1982; Watt 1986). The greater the scope for activity, the greater the available energy for feeding, digestion, osmoregulation and active behaviours such as foraging, migration, territorial defence and courtship behaviours. Differences in scope for activity between individuals may translate into differences in foraging/migration range, growth rate, and reproductive success (Beamish and Trippel 1990).

Apparent Specific Dynamic Action (SDA) may provide another useful index of the potential fitness of individuals. SDA is the energetic cost of processing food (i.e.

ingestion, digestion and absorption) and is characteristically observed as a postprandial increase in oxygen consumption of the fish, resulting in a temporary reduction in aerobic scope (see Chapter 1). This reduction in the scope for activity may limit further foraging or spawning behaviour and may place the fish at a greater risk of predation or competitive exclusion (Vahl and Davenport 1979). Information about the intraspecific variation of SDA might be used to predict individual foraging or spawning patterns and, by extension, rates of growth and reproductive output. It is widely held that natural selection will favour energetic efficiency in the conversion of food into reproductive output (King and Roughgarden 1982; Schaffer et al. 1982; Chiariello and Roughgarden 1984; Iwasa and Roughgarden 1984; Watt 1986). While several studies have investigated the effects of food conversion efficiencies on growth and reproductive outputs of plants (King and Roughgarden 1982; Schaffer et al. 1982; Chiariello and Roughgarden 1984; Iwasa and Roughgarden 1984), this approach has rarely been taken by zoologists.

In demersal marine fishes, potential fitness is closely linked to growth. Sexual maturation in demersal fishes is generally more closely related to size than to age (Jones 1991). Growth rate will therefore determine how early a fish begins reproducing. Moreover, fecundity increases as a power of length (Munro 1983; Polovina and Ralston 1986; Roberts and Polunin 1991; Medley et al. 1993). Thus, faster growing individuals may have a higher fitness than slow-growing individuals. This is particularly likely given that survival of juvenile fish is generally size-specific, with small, slow-growing individuals suffering heavier mortality (Post and Evans 1989; Juanes 1994; Chapter 4). Growth of juvenile fish may be closely linked to their individual scope for activity and/or

apparent SDA, as individuals with surplus energy remaining after expenditure on daily activities and digestion may allocate that energy to somatic growth.

The purpose of this chapter is to measure intraspecific variation in growth rates and metabolic costs of foraging in juvenile cunner (Tautoglabrus adspersus) and to determine if a relationship exists among growth rates, scope for activity and SDA of individual fish.

METHODS

Growth rates

Newly settled cunner were captured in August, 1992, from Back Cove Reef in St. Margarets Bay, Nova Scotia using anaesthetic (10% solution of quinaldine sulfate (Sigma) in seawater). Captured fish were marked with acrylic dye, using a specific pattern of coloured dots (allowing individual fish to be recognized and measured by visual estimation in subsequent censuses), and immediately returned to their capture site. Upon release, the fish invariably returned immediately to their original shelter site. This procedure took less than 3 minutes per fish and was completed in situ, without removing the fish from the water. Marked individuals were recaptured and remeasured at biweekly intervals from Sept. 1 to Dec. 21, 1992. A total of 36 individuals were captured and marked. However, due to the high mortality inherent in newly settled fish (Sale and Ferrell 1988; Connell and Jones 1991), a complete record of recaptures and measurements was only available for 10 individuals.

Scope for activity

The 10 individual cunner for which growth data were collected in the previous section were captured in late December using a 10% solution of anaesthetic (quinaldine sulfate (Sigma) in seawater, and brought to the laboratory where they were kept overwinter at about 3°C above ambient temperature and at ambient photoperiod. Cunner remained torpid from December until May, 1993. In June, cunner were acclimated, without feeding, to 15°C for 4 weeks prior to experimentation. Experimental animals ranged from 30-60 mm total length and 3.6-11.3 g weight weight. All experiments were conducted at 15°C, which approximated summer temperatures in St. Margarets Bay. The respirometric apparatus used to determine scope for activity and apparent SDA is described in Chapter 1.

To determine the standard and active metabolic rate and scope for activity of individual cunner, unfed fish were placed in the respirometer chamber at a flow speed of 1 cm s⁻¹ and left overnight (16 h) to adjust to the chamber and the flow. Oxygen consumption was then measured in 30 min runs over a range of incrementally increased swimming speeds. When the fish could no longer hold station against the current, the experiment was terminated, and the fish was removed from the respirometer and weighed. The respirometer chambers were emptied and refilled after each run. Each individual underwent the procedure three times, with a 2 week rest between runs on the same individual. Blanks (no fish in chamber) were run before and after each experimental run; the baseline oxygen consumption of the probe, and of any microorganisms present in the

chamber, was then subtracted from the total rate of oxygen depletion. Oxygen consumption was regressed on swimming speed (converted to body lengths sec^{-1}) for each individual; the resulting equations were used to calculate the active metabolic rate, i.e. the oxygen consumption at the critical swimming speed (determined as per Brett 1964) and to extrapolate the standard metabolic rate, i.e. the oxygen consumption at the y intercept of the equation. Scope for activity was calculated as the difference between active and standard metabolic rates.

Apparent SDA

The amplitude and duration of apparent SDA were measured for the same 10 individual cunner as above (30-60 mm total length; 3.6-11.3 g wet weight). In each run, a cunner was placed in each of the two respirometer chambers, which was set at a flow speed of 1.5 cm s^{-1} . The fish were left overnight to allow them to adjust to the chamber. After the fish had acclimated to the chamber, 0.2 g of finely chopped shrimp suspended in seawater was pipetted into one chamber through the hole in the lid (see Chapter 1). The fish in the second chamber was not fed. The oxygen probe was inserted into the first chamber, and the decline in oxygen tension over a 30 min period was measured at 0-6, 8, 10, 12, 16, and 24 hours post-feeding. Because the respirometer could not be flushed between each 30 min period, a pilot experiment was performed which determined that the oxygen tension did not decrease sufficiently to adversely affect the fish (Haugaard and Irving 1947). The individual was then removed from the respirometer and weighed. The

oxygen probe was then transferred to the second chamber, and the oxygen consumption of the unfed fish was measured according to the same schedule. All 10 individuals were subjected to both fed and unfed treatments, with a 2 week starvation period between treatments.

Analysis of data

Prior to analysis, all numeric data were subjected to normal probability plots (Wilkinson 1990) and Bartlett's Test for homogeneity of variance (Sokal and Rohlf 1981). Where necessary, data were log transformed to meet the assumptions of regression and analysis of variance. Linear regressions were used to relate swimming speed to oxygen consumption. The slopes of these regressions represent the metabolic cost of locomotion; regression slopes were compared using a test for homogeneity among slopes of several regressions (Sokal and Rohlf 1981).

The magnitude of SDA was calculated for each run by averaging the amplitude between two successive points on the oxygen consumption curve and multiplying the average amplitude (Δy) by the time separating the two points (Δx). The area under each successive pair of points was calculated in this fashion; the sum of these areas, i.e. the total area under the curve, minus the oxygen consumption due to standard metabolic rate, represented the magnitude of apparent SDA (see Chapter 1). Intraspecific variation in scope for activity and in the magnitude of apparent SDA was investigated by analysis of variance. Where significant variation occurred, a pairwise multiple

comparison test (Tukeys' HSD) was used to identify significant differences between individuals. Correlational analyses (Pearson product-moment correlation coefficient) were used to relate scope for activity and magnitude of apparent SDA to individual growth rates.

RESULTS

Settlement and growth

Settlement of 0+ cunner occurred over a short period of time (21 days) in late August, 1992 (Chapter 4). Newly settled cunner inhabited crevices in the reef substrate and remained site-attached, defending territories around their home site. Encounters between 0+ cunner along the boundaries generally resulted in aggressive interactions. In all cases where a visible size difference existed between the interacting fish, the larger individual succeeded in driving away the smaller. Figure 5.1 illustrates the increase in total length of 10 individual 0+ cunner at Back Cove Reef, determined by successive recapture. As demonstrated in Chapter 4, there was a tendency for individuals that were larger at settlement to remain larger throughout the study period, while individuals that were smaller at settlement tended to remain smaller. Unfortunately, it was not possible to test for statistically significant differences in individual growth rates, as the variation in growth with temperature confounded the replicate growth measurements of individuals, and successive measures of individual length are not statistically independent. Post-

Fig. 5.1 Variation in water temperature and the temporal increase in total length of 10 individual 0+ cunner at Back Cove Reef (determined by mark/recapture) from August 27 to Dec. 14, 1992.

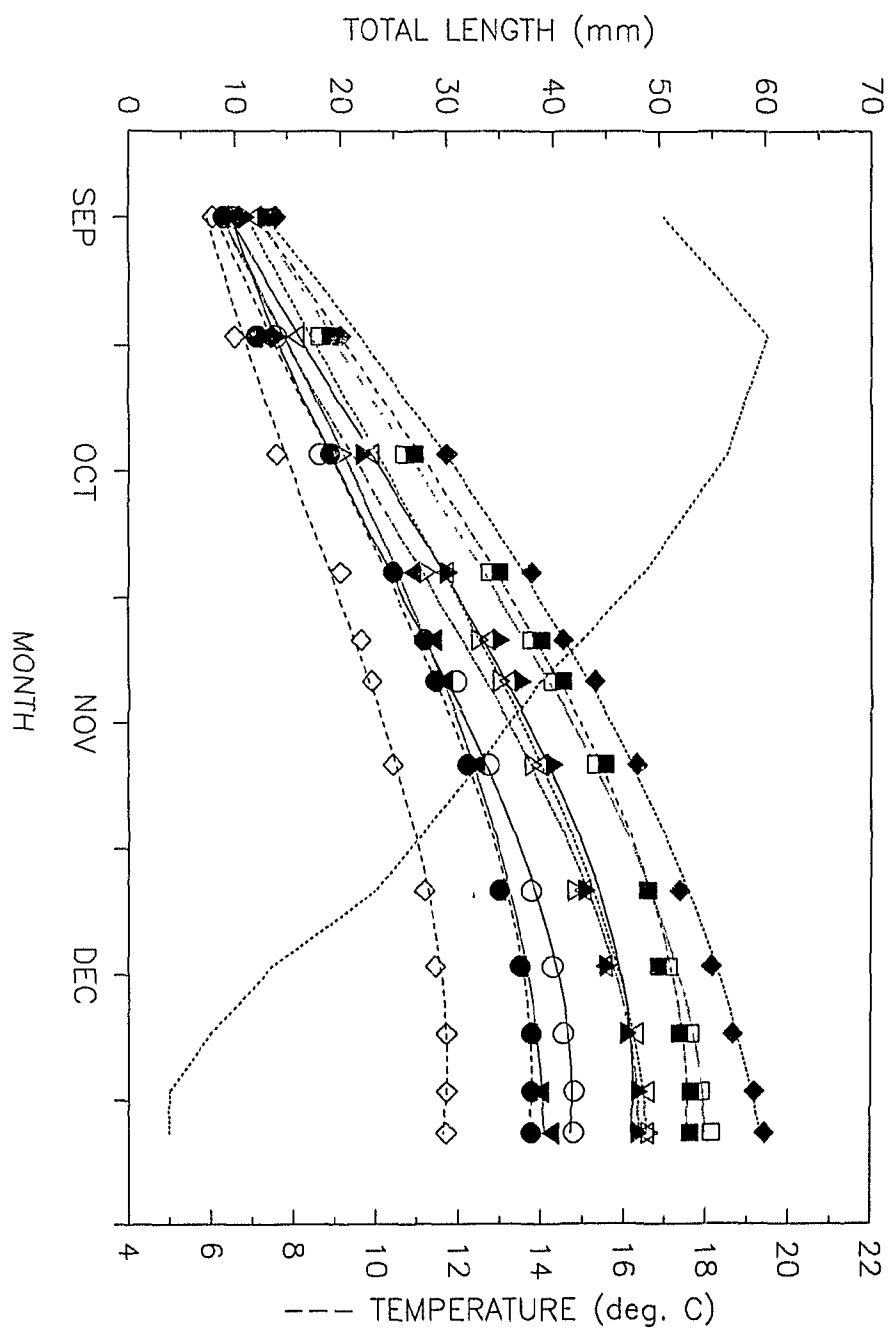


Fig. 5.1

settlement growth rates of individual cunner increased with temperature from 0 mm day⁻¹ at 5°C to 0.15-0.75 mm day⁻¹ (mean = 0.56 mm day⁻¹) at 18.8°C (Fig. 5.2). Maximum growth of 0+ cunner occurred in mid September, coinciding with maximum water temperature. After September, growth rate declined steadily until December, at which point no further increases in length were recorded. As temperatures decreased, 0+ cunner became less active and spent more time resting in shelter sites (Fig. 2.1). By late December, at a temperature of about 4°C, all cunner had become dormant.

Scope for activity

Figure 5.3 illustrates the relationship between oxygen consumption and swimming speed. A separate regression was fitted for each individual; the slopes of these regressions represent the metabolic cost or efficiency of locomotion. A test for homogeneity of slopes between regressions found no significant differences in the cost of locomotion between individual cunner ($F = 1.87$, $p > 0.05$).

Scope for activity of individual cunner is shown in Fig. 5.4. The scope for activity also did not differ significantly between individuals (ANOVA, $F = 1.69$, $p > 0.05$). In summary, 0+ cunner from the Back Cove population showed very little intraspecific variation in either the cost of locomotion or the scope for aerobic activity.

Fig. 5.2 Effects of temperature on in situ growth rate of 10 individual 0+ cunner from Back Cove Reef. Growth rates were calculated from successive recaptures and measurements of marked individuals.

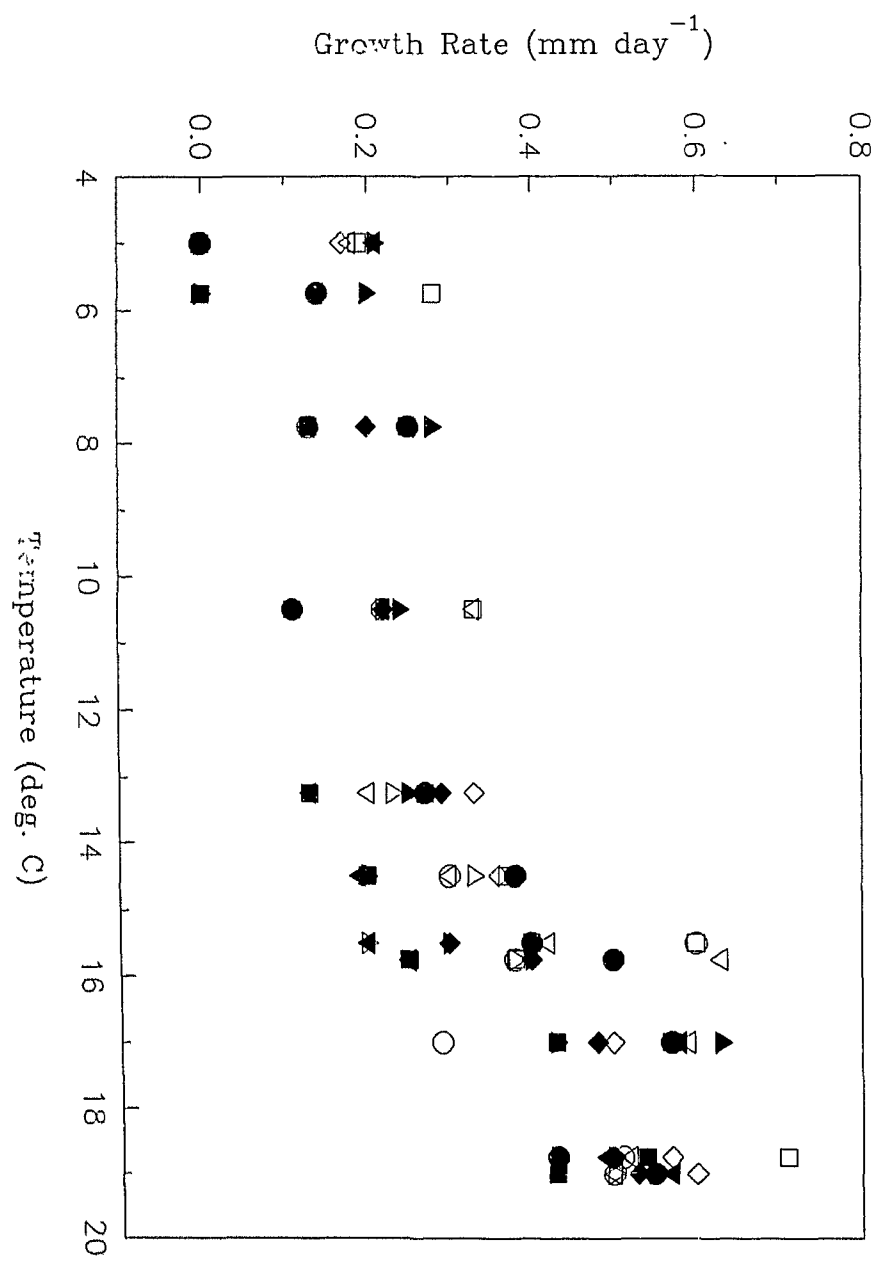


Fig. 5.2

Fig. 5.3 The relationship between oxygen consumption and swimming speed of 10 individual 0+ cunner. Standard metabolic rates of each individual are extrapolated from the y intercept of the regression lines. The slope of each line represents the energetic cost of locomotion.

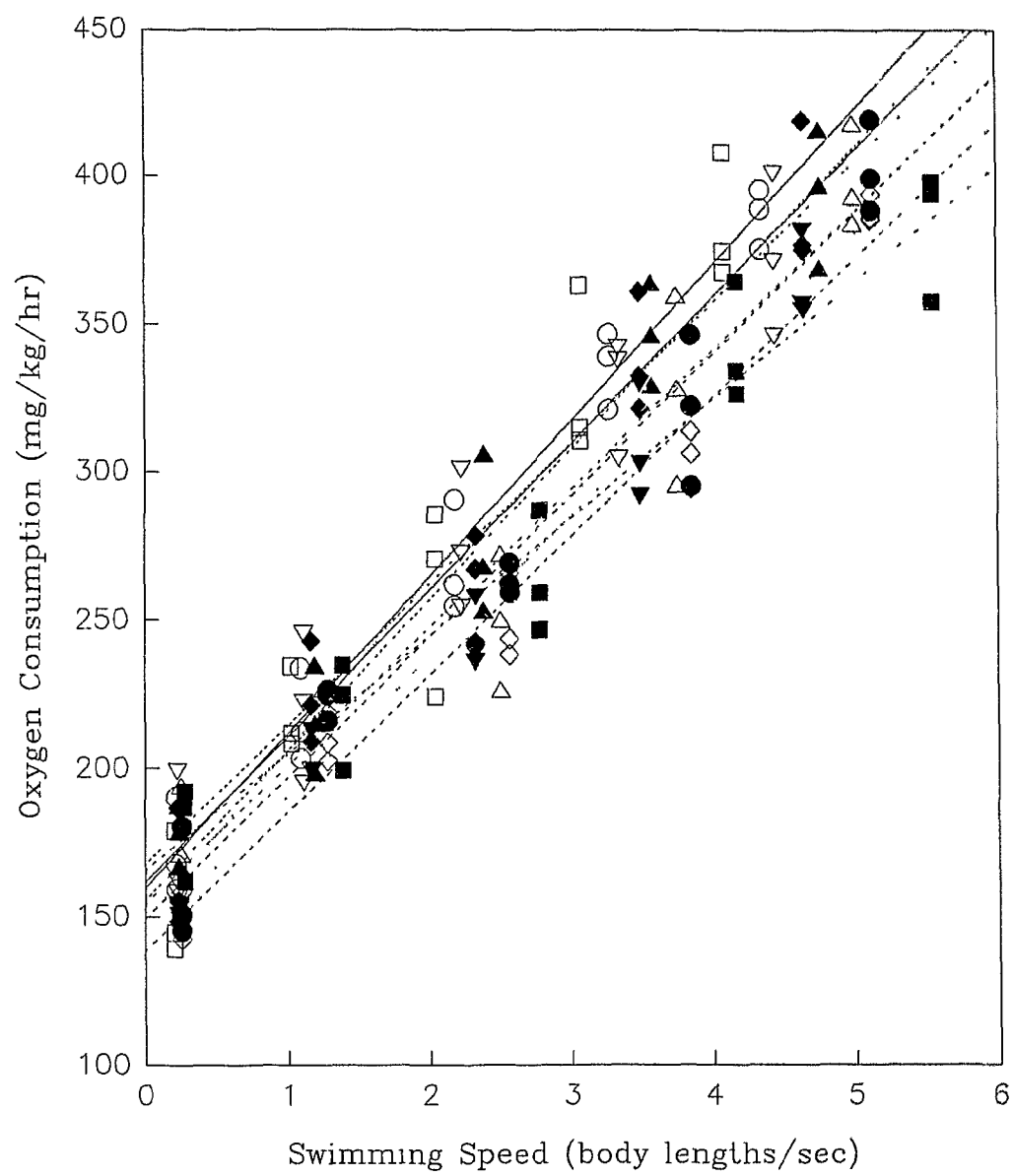
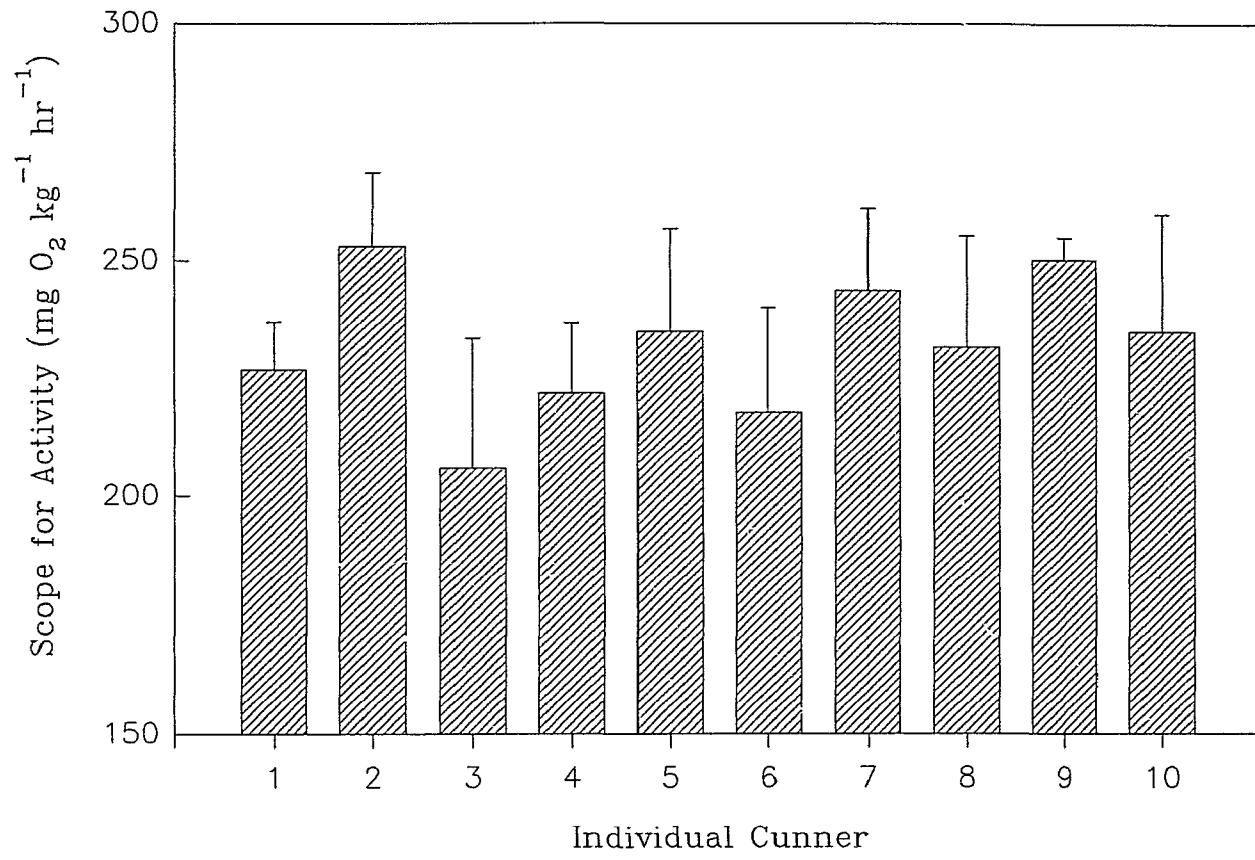


Fig. 5.3

Fig. 5.4 Scope for activity of 10 individual 0+ cunner (3 repeated measures per individual) from Back Cove Reef. Vertical error bars represent ± 1 standard deviation.

Fig. 5.4



Apparent specific dynamic action

Oxygen consumption of unfed cunner (controls) is shown in Fig. 5.5. The amplitude and duration of apparent SDA are illustrated for the same individuals after feeding in Figure 5.6. Intraspecific differences are apparent in both the peak amplitude of oxygen consumption and the length of the postprandial effect. The magnitude of apparent SDA was calculated for each individual cunner (Fig. 5.7a) and significant differences were found between individuals (ANOVA, $F = 143.3$, $p < 0.0001$). Magnitude of apparent SDA will be a more useful index of fitness when expressed as a proportion of scope for activity (Fig. 5.7b). An animal with a low SDA, which is energetically efficient in terms of foraging, may be less 'fit' than an animal with a higher SDA but a proportionately higher scope for activity. However, since scope for activity did not differ between individual cunner, it is not surprising that a similar pattern of significant intraspecific variation (ANOVA, $F = 32.8$, $p < 0.001$) was found when the magnitude of SDA was expressed as a percentage of scope for activity (Fig. 5.7b).

Prediction of growth

Growth rate of individual 0+ cunner was unrelated to scope for activity ($r = 0.01$, $p > 0.95$; Fig. 5.8a), as would be expected since scope for activity did not vary among individuals. However, growth rate was negatively correlated with the magnitude of apparent SDA when expressed in absolute cost ($r = -0.87$, $p < 0.0001$) and as a proportion

Fig. 5.5 Oxygen consumption of unfed (control) individual 0+ cunner (3 repeated measures per individual) swimming at 1.5 cm s^{-1} . Vertical error bars represent ± 1 standard deviation.

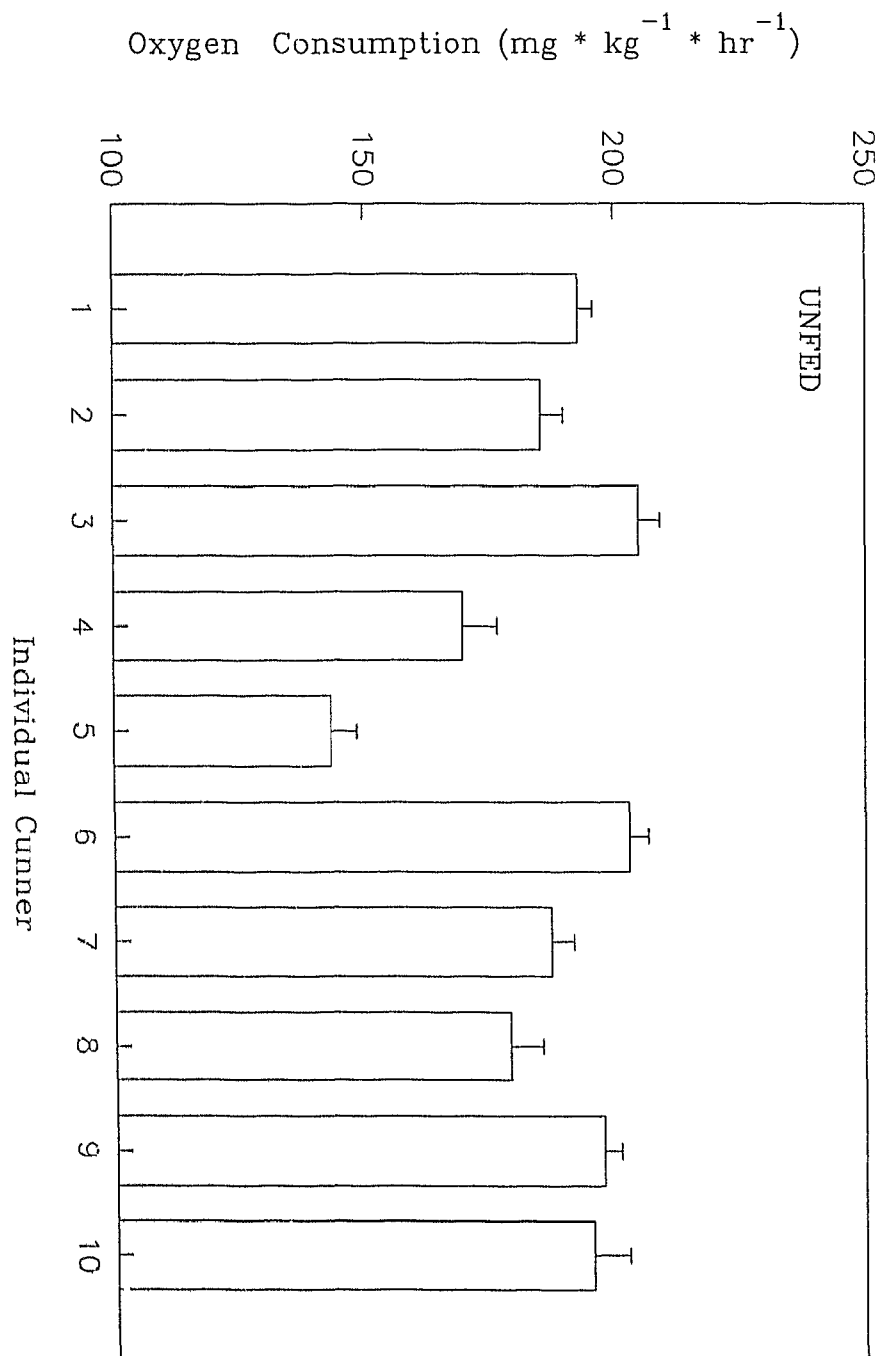


Fig. 5.5

Fig. 5.6 Oxygen consumption over a 24 hr time period of 10 individual 0+ cunner fed 200 mg of chopped shrimp at time = 0. Vertical error bars represent ± 1 standard deviation.

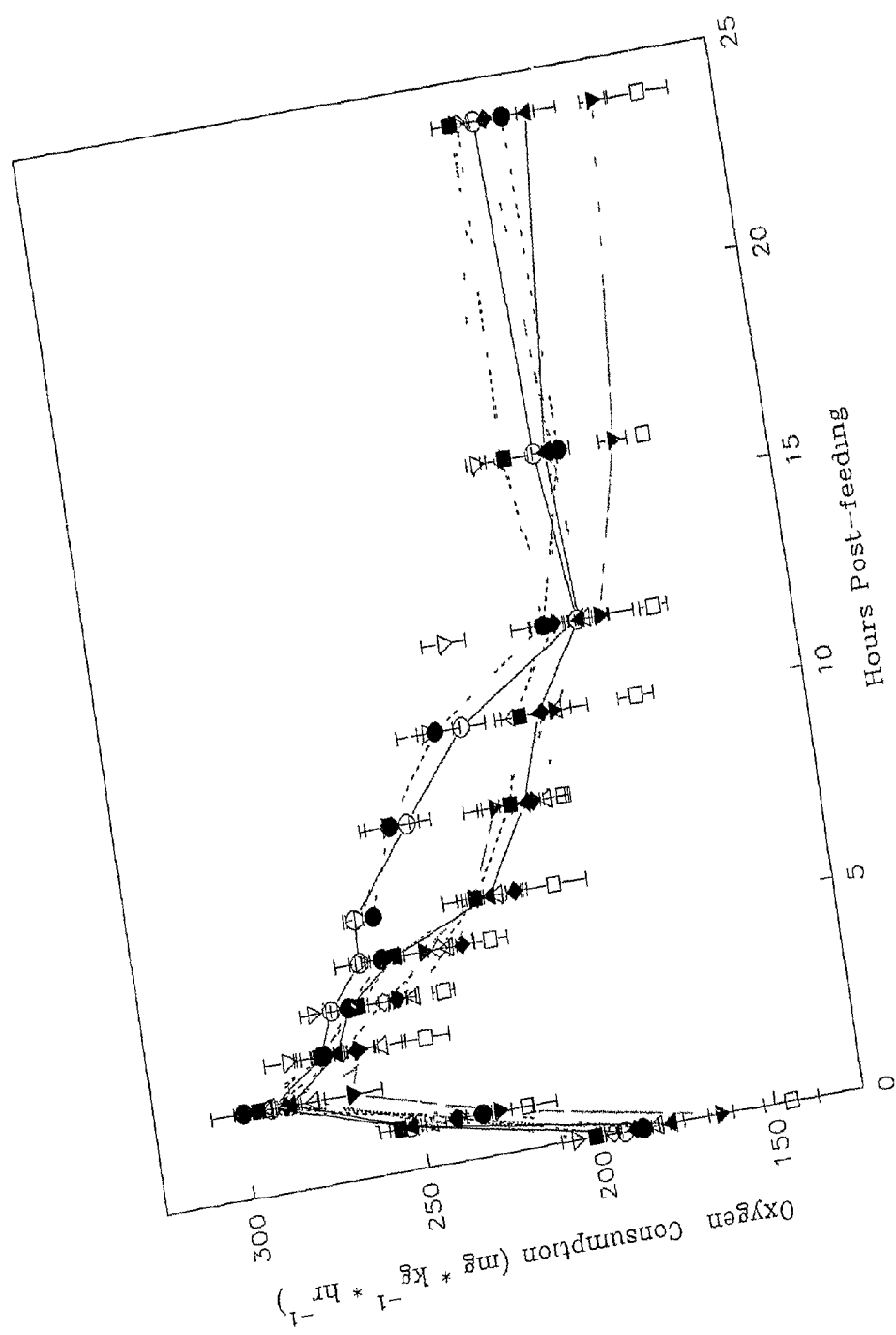


Fig. 56

Fig. 5.7 Magnitude of apparent SDA for 10 individual 0+ cunner. (a) Absolute value of magnitude. (b) Magnitude of SDA as a percentage of scope for activity (magnitude of SDA over a 12 hr duration was divided by aerobic scope over same period, i.e. magnitude of SDA / (aerobic scope x 12)). Vertical error bars represent ± 1 standard deviation.

Fig. 5.7

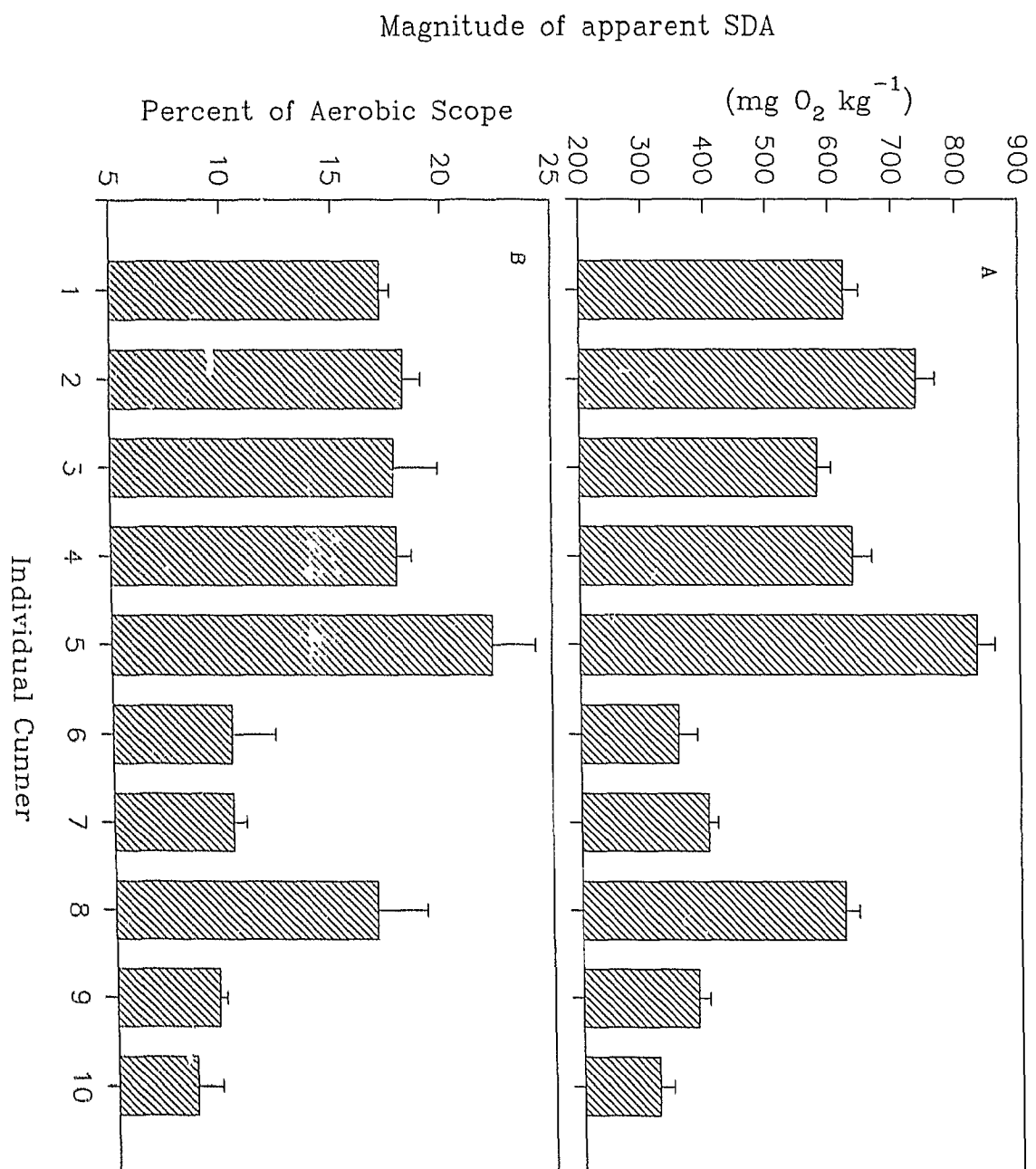


Fig. 5.8 Relationship of growth rate of 10 individual 0+ cunner to (a) absolute scope for activity, and (b) metabolic cost of foraging (i.e. magnitude of SDA) as a percentage of scope for activity. Growth rate was calculated as the mean increase in length (mm day^{-1}) over the previous summer (see Fig. 5.1).

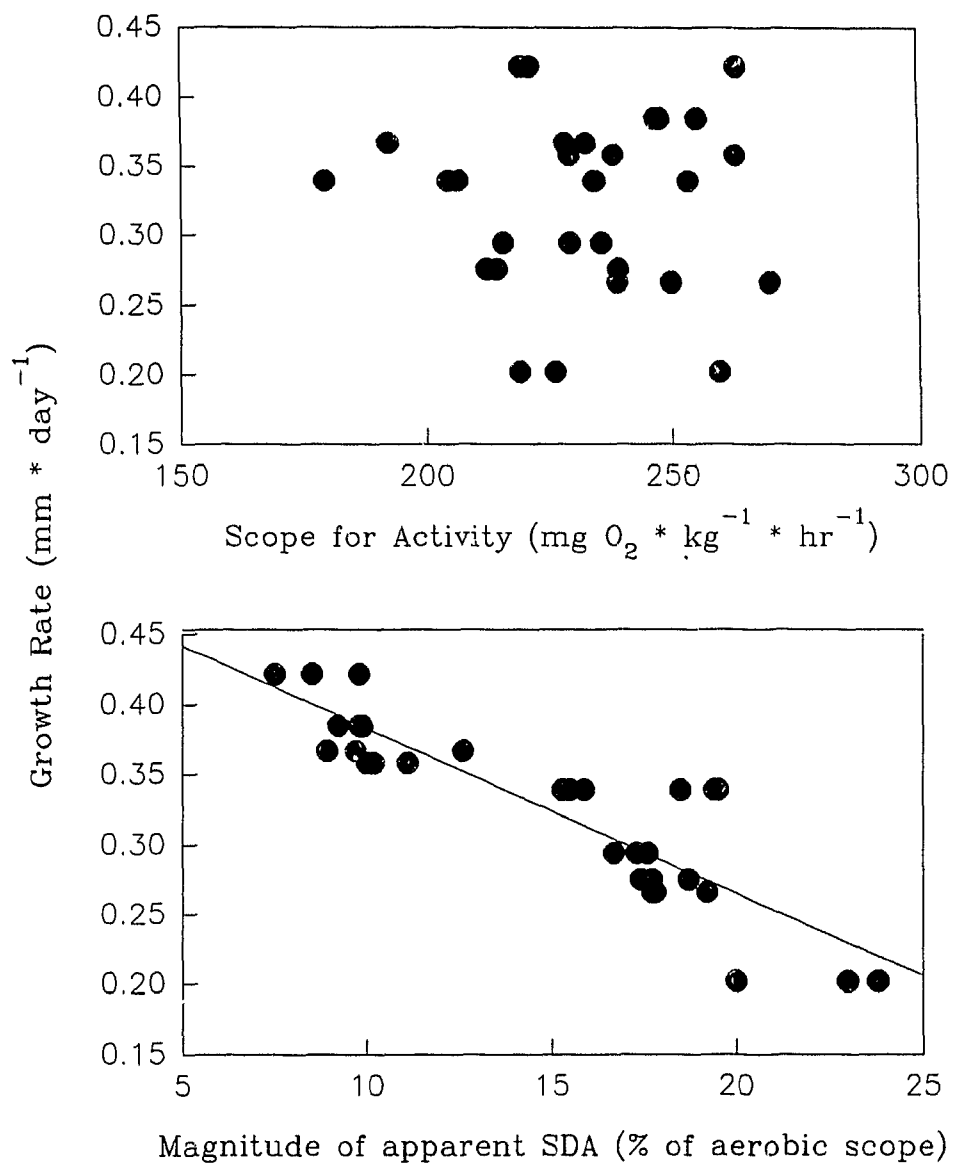


Fig. 5.8

proportion of scope for activity ($r = -0.78$, $p < 0.0001$; Fig. 5.8b). Thus it appears that intraspecific variation in growth of cunner might be better predicted by the energetic efficiency of foraging and growth processes, rather than by the absolute amount of available energy.

DISCUSSION

Individual growth rates of 0+ cunner varied from 0.20-0.42 mm day⁻¹; cunner that were larger at settlement grew more rapidly than small settlers (Fig. 5.1). While this type of growth depensation is common among newly settled demersal fishes (Forrester 1990; Tupper and Boutilier 1994), the underlying mechanisms remain unclear. In some species, growth depensation occurs only when food is limiting (Magnuson 1962), while in others, growth depensation occurs even when food is in adequate supply (Jobling 1985). In the latter case, density-dependent behavioural interactions are thought to either decrease the rate of food consumption or increase the rate of energy expenditure, particularly of smaller individuals (Wootton 1990). In 0+ cunner, increases in conspecific density cause a reduction in the rate of foraging and an increase in energy expenditure on shelter site defense (Table 2.5a,b). This leads to density-dependent growth depensation, in which the mean growth rate of the population is depressed (Fig. 3.2c), but growth rate of the largest individuals (i.e. the best competitors) decreases relatively little (Figs. 3.3, 5.1; Tupper and Boutilier 1994).

Aerobic scope for activity is considered to be important to survival of teleost fishes,

as it governs the amount of energy available for many life-sustaining activities (Fry 1947, 1971). Scope for activity has been studied in the context of energetic efficiency: for a given caloric intake, those animals that expend energy at a low proportion of aerobic scope maximize their surplus energy, which can be allocated to growth or reproduction (Priede 1985). Thus, individuals that inherit the metabolic traits necessary to maximize aerobic scope should enjoy a distinct competitive advantage over other conspecifics. It should be noted however, that fishes with differing natural histories may have different metabolic requirements. Certainly, fish species differ in their scopes for activity (Fry 1971; Beamish 1978; Vahl and Davenport 1979; Soofiani and Priede 1985); pelagic species (e.g. scombrids and tunnids) that are adapted for prolonged high-speed cruising have much higher scopes for activity than sedentary reef fish or benthic ambush predators (Muir and Niimi 1972; Priede 1985). Within the Back Cove Reef cunner population, no significant intraspecific differences were found in either the energetic cost of locomotion or scope for activity. Thus, growth rates of individual cunner were unrelated to these metabolic traits. Given the sedentary nature of 0+ cunner, which forage at low speeds (Fig. 2.2) within home ranges of about 1-5 m² (personal observations), it is perhaps not surprising that swimming efficiency had little bearing on surplus energy and growth.

Regarding scope for activity, growth may be constrained less by the absolute difference between standard and active metabolic rate than by the proportion of scope for activity allocated to various metabolic costs, such as foraging and shelter site defense. More simply stated, growth may rely primarily on the scope for activity remaining after energy requirements of all daily activities have been fulfilled. Hoppeler and Turner

(1989) suggested that although the metabolic cost of maintaining the respiratory machinery necessary for a larger aerobic scope is low, many animals appear to be optimized for their average daily energy expenditure rather than for their active metabolic rate. They speculated that animals in nature rarely perform activity at VO_{2max} , and that highly active behaviours such as predator avoidance or territorial defense are primarily fuelled by anaerobic metabolism.

As was the case in this study, individuals with identical scopes for activity may differ in growth rate if there is significant variation in SDA. In 0+ cunner, the magnitude of apparent SDA, both in absolute terms and as a proportion of scope for activity, was inversely related to growth rate. This suggests that individuals with a lower SDA had more surplus energy to spend on somatic growth. Jobling (1981) described apparent SDA as the "inescapable cost of growth", since the majority of the postprandial increase in oxygen consumption appears to be caused by protein digestion and resynthesis. Thus, SDA can be considered a measure of growth efficiency. Indeed, in this study, individuals for which the cost of growth was low were those that grew most rapidly. Since survival of newly settled cunner has been demonstrated to be size-dependent, favouring larger individuals (Fig. 3.4), it appears that the metabolic cost of foraging (i.e. apparent SDA) may be a useful indicator of survival as well as growth.

The fact that faster-growing fish not only had lower magnitudes of apparent SDA but were also larger at settlement begs the question: if larger sizes at settlement are the result of faster larval growth rates, are growth rates of planktonic larvae similarly affected by apparent SDA? Intuitively, if the magnitude of SDA is a heritable trait, intraspecific

variation should be present throughout the life history, unless abnormal values of SDA are selected against. Recent advances in molecular genetics have enabled the production of DNA 'fingerprints' that are capable of identifying individual organisms (Jeffreys et al. 1985). Using this technology to identify genotypic differences in foraging efficiency (i.e. differences in the magnitude of SDA), it might be possible to predict growth and survival of early life history stages of fish: an exciting prospect to fisheries biologists concerned with recruitment forecasting.

GENERAL CONCLUSIONS

Variation in first-year survival of juvenile fishes can be attributed to either pre-settlement or post-settlement processes, or events occurring during transition from the pelagic to demersal existence (Jones 1990, 1991; Kaufman et al. 1992; Tupper and Hunte 1994). Pre-settlement processes affect the survival of planktonic larvae (generally through the influence of hydrographic regimes) and are outside the scope of this thesis. Processes occurring at settlement include microhabitat selection (McFarland 1979; Sale 1984), and rapid ontogenetic shifts in foraging and predator avoidance behaviour (Kaufman et al. 1992). Post-settlement survival appears most closely linked with predation rates and competition for limited refugia (Shulman et al. 1983; Shulman 1984, 1985a,b; Shulman and Ogden 1987; Chapter 4). In addition, survival of newly settled fish is strongly size-dependent (Post and Evans 1989a; Juanes 1994; Chapter 3). Thus, factors affecting growth are central to determining recruitment success of juvenile fishes. In addition to food availability, variation in the allocation of resources (specifically time and energy) to maintenance and activity will determine a fishes' potential for growth (Schoener 1971; Ware 1982). Allocation of resources may be strongly influenced by abiotic variables such as temperature, hydrographic regimes and physical habitat structure, as well as by biotic variables, including predation risk, density of conspecific or heterospecific competitors and prey density (Wootton 1990).

For cunner, as for other fish species (Priede 1985), the maximum energy expenditure of each component of the daily energy budget (resting, foraging and shelter site defense)

can sum to a value much higher than the active metabolic rate. Energy can thus be considered a resource that can limit population size. Cunner must allocate energy to each component so that the scope for activity is not exceeded. The pattern of allocation should serve to maximize the animals' growth and survival (Ware 1982; Watt 1986). For newly settled fish, in which rapid growth is essential to survival (Post and Evans 1989a; Juanes 1994), energy expenditure should be kept to a minimum so that surplus energy may be directed toward growth (Priede 1985). Under natural conditions, cunner operate at a low proportion of their scope for activity (Table 2.1), although a peak of activity and apparent SDA late in the day can substantially reduce surplus power (Figs. 2.4, 2.5). This late-day reduction in surplus energy may be related to the evolution of nocturnal torpor in cold-temperate labrids (i.e. cunner and tautog Tautoga onitis).

Temperature affects all components of the energy budget and therefore affects the allocation of energy among these components. Swimming capacity and scope for activity are greatly reduced at low temperatures. Thus, large investments of energy into foraging and shelter site defense are not possible at low temperatures. This may partially explain the existence of overwinter hibernation in cunner.

Competition for shelter sites is an important component of the energy budget of cunner and can account for almost the entire scope for activity when shelter is limiting. At high population densities, shelter sites become limiting and cunner invest large amounts of time and energy in acquiring and defending these sites (Tables 2.4, 2.5a,b). In addition, the increased time spent defending shelter sites results in less time spent foraging (Table 2.3). This greatly reduces the surplus energy available for growth, as

evidenced by the strong density-dependence of growth observed in this study (Figs. 3.2c, 3.6b). High densities of conspecifics also reduce post-settlement survival. The primary mechanism behind density-dependent survival is likely to be increased predation risk to individuals unable to occupy shelter sites. Moreover, since piscivores actively select smaller size classes (Juanes 1994), a decrease in mean growth rate at high densities may increase predation risk of the population as a whole.

If a given habitat type offered an advantage in terms of reduced energy expenditure, then one might expect a fish to select that habitat whenever possible. In this study, no particular energetic advantage was offered by any of the available habitats (Table 2.3a,b), and cunner showed no evidence of microhabitat selection at or following settlement (Fig. 4.3). Instead, cunner settled uniformly in all habitats and remained tenaciously site-attached after settlement. Differential predation pressure, however, resulted in variation of recruitment success among habitats. Predators were less successful at capturing newly settled cunner in topographically complex habitats, such as rocky reefs and cobble bottoms. Levin (1993, 1994a) also found that, in cunner, differential mortality tended to decouple settlement from subsequent recruitment success. Regulation of demersal fish populations by pre-settlement vs post-settlement processes have been the subject of vigorous debate for the last decade, and a number of competing hypotheses have been advanced (Doherty 1982, 1983; Shulman et al. 1983; Victor 1983, 1986; Shulman 1984, 1985a; Jones 1986, 1987a; Hixon 1991). It appears that the population dynamics of cunner are best explained by the 'predation hypothesis' (Hixon 1991), which predicts that abundance will be inversely related to predation pressure.

Growth rates of 0+ cunner also differed between habitats, but the pattern of variation was not the same as for predation and mortality. Growth was highest in seagrass beds and lowest on reef and cobble (Fig. 4.10). Although no direct measures of prey density were available, the variation in growth was attributed to food quantity and quality. Levin (1994b) demonstrated that spatial variation in the abundance of cunner recruits in the Gulf of Maine was closely linked to prey distribution. In contrast, recruit abundance in St. Margarets' Bay was less influenced by prey density and growth than by habitat structure and its effects on predation pressure. However, since mortality is size-dependent, seagrass beds may share equal importance with reef and cobble habitats in supplying recruits to subsequent year-classes. Newly settled cunner face trade-offs between energy gain (growth) and predation risk (mortality). A possible scenario is that seagrass beds produce fewer, larger individuals, each with a higher chance of survival (Post and Evans 1989a; Juanes 1994), while hard-bottom habitats produce more, smaller individuals, each with a lower chance of survival. The implications of these trade-offs to population regulation are unclear (Walters and Juanes 1994; Tupper and Boutilier unpubl. ms) but clearly merit further investigation.

Given that size-dependent mortality has been demonstrated for cunner (Fig. 3.4), as for many other species (Juanes 1994), growth rates of individual fish may be good predictors of their survival probability. Intraspecific variation in growth is a common phenomenon among fishes (Weatherley and Gill 1987), and growth depensation (increasing variance in growth rates over time) has been demonstrated in situ for some demersal species (Forrester 1990; Tupper and Boutilier 1994; this study). Growth is

essentially a biochemical process (Jobling 1981); rates of growth are closely tied to the surplus power available to drive biochemical reactions (Watt 1986). However, growth rate was not related to an animals' scope for activity per se (i.e. the difference between active and standard metabolic rates). Instead, individual rates of growth were found to be related to the amount of aerobic scope remaining after the metabolic costs of foraging had been met. Animals with low apparent SDA in relation to their scope for activity appeared able to channel their surplus energy into growth. Since animals that are large at settlement are likely to be the same fast-growing juveniles that suffer lower mortality rates than smaller individuals, genetic techniques that focus on the heritability of SDA and other processes involved in growth, should prove useful in predicting the survival and eventual recruitment success of juvenile fishes.

LITERATURE CITED

- Aldenhoven, A. J. (1986). Local variation in mortality rates and life-expectancy of the coral-reef fish Centropyge bicolor (Pisces, Pomacanthidae). Mar. Biol. 92: 237-244.
- Arnold, S. J. (1987). Genetic correlation and the evolution of physiology. In Feder, M. E., Bennett, A. F., Burggren, W. W., Huey, R.B. (eds.) New Directions in Ecological Physiology. Cambridge Univ. Press, N.Y. p. 189-215.
- Arnold, S. J. (1988). Behaviour, energy and fitness. Am. Zool. 28: 815-827.
- Auster, P. J. (1989). Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic and Mid-Atlantic). Tautog and cunner. Biol. Rep. U.S. Fish Wildl. Serv. 82(11.105) TR EL-82-4. 13 p.
- Beamish, F. W. H. (1974). Apparent specific dynamic action of largemouth bass, Micropterus salmoides. J. Fish. Res. Bd. Can. 31: 1763-1769.
- Beamish, F. W. H. (1978). Swimming capacity. In Hoar, W. S., Randall, D. J. (eds.) Fish Physiology, vol. VII. Academic Press, London, p. 101-187.
- Beamish, F. W. H., Trippel, E. A. (1990). Heat increment: a static or dynamic dimension in bioenergetic models? Trans. Am. Fish. Soc. 119: 649-661.
- Behrents, K. (1987). The influence of shelter availability on recruitment and early juvenile survivorship of Lythrypnus dalli Gilbert (Pisces: Gobiidae). J. Exp. Mar. Biol. Ecol. 107: 45-59.

- Bell, J. D., Galzin, R. (1984). Influence of live coral cover on coral-reef fish communities. *Mar. Ecol. Prog. Ser.* 15: 265–274.
- Bigelow, H. B., Schroeder, S. C. (1953). Fishes of the Gulf of Maine. *Fish. Bull. U.S. Fish Wildlf.*, Vol. 53. U.S. Government Printing Office, Washington. 577 p.
- Björnsson, B. (1985). Bioenergetics of cod (Gadus morhua L.): a response to food intake with possible implications for fisheries management. Ph.D. thesis, Dalhousie Univ., Halifax, N.S.
- Boisclair, D., Leggett, W. C. (1989a). The importance of activity in bioenergetics models applied to actively foraging fishes. *Can. J. Fish. Aquat. Sci.* 46: 1859–1867.
- Boisclair, D., Leggett, W. C. (1989b). Among population variability of fish growth: I. Influence of the quantity of food consumed. *Can. J. Fish. Aquat. Sci.* 46: 457–467.
- Bolz, G. R., Lough, R. G. (1988). Growth through the first six months of Atlantic cod, Gadus morhua, and haddock, Melanogrammus aeglefinus, based on daily otolith increments. *Fish Bull.* 86: 223–235.
- Breitburg, D. (1989). Demersal schooling prior to settlement by larvae of the naked goby. *Env. Biol. Fish.* 26: 97–103.
- Breitburg, D. (1991). Settlement patterns and presettlement behaviour of the naked goby, Gobiosoma boscii, a temperate oyster reef fish. *Mar. Biol.* 194: 221–231.
- Brett, J. R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd. Can.* 21: 1183–1226.

- Brett, J. R., Groves, T. D. D. (1979). Physiological energetics. In Hoar, W. S., Randall, D. J., Brett, J.R. (eds.) Fish Physiology, vol. VIII. Academic Press, London, p. 279–352.
- Brown, J. L. (1964). The evolution of diversity in avian territorial systems. *Wilson Bull.* 76: 160–169.
- Brown, J. A., Pepin, P., Methven, D. A., Somerton, D. C. (1989). The feeding growth and behaviour of juvenile cod, Gadus morhua L., in cold environments. *J. Fish Biol.* 35: 373–380.
- Calow, P. (1977). Conversion efficiencies in heterotrophic organisms. *Biol. Rev.* 52: 385–409.
- Campana, S. E., Frank, K. T., Hurley, C. F., Koeller, P. A., Page, F. H. and Smith, P. C. (1989). Survival and abundance of young Atlantic cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) as indicators of year-class strength. *Can. J. Fish. Aquat. Sci.* 46, 171–182.
- Carr, M. H. (1991). Habitat selection and recruitment of an assemblage of temperate zone reef fishes. *J. Exp. Mar. Biol. Ecol.* 146: 113–137.
- Chandler, C. R., Sanders, R. R. Jr., Landry, A. M. Jr. (1985). Effects of three substrate variables on two artificial reef fish communities. *Bull. Mar. Sci.* 37: 129–142.
- Chao, L. N. (1973). Digestive system and feeding habits of cunner, Tautoglabrus adspersus, a stomachless fish. *U.S. Natl. Mar. Fish. Serv. Fish. Bull.* 71: 565–586.
- Chiariello, N., Roughgarden, J. (1984). Storage allocation in seasonal races of annual plant: optimal vs actual allocation. *Ecology* 65: 1290–1301.

- Connell, S. D., Jones, G. P. (1991). The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *J. Exp. Mar. Biol. Ecol.* 151: 271–294.
- Cowen, R. K. (1991). Variation in the planktonic larval duration of the temperate wrasse Semicossyphus pulcher. *Mar. Ecol. Prog. Ser.* 69: 9–15.
- Coutant, C. C., Benson, D. L. (1985). Summer habitat suitability for striped bass in Chesapeake Bay: reflections on a population decline. *Trans. Am. Fish. Soc.* 119: 757–778.
- Crawshaw, L. I., Moffitt, B. P., Lemons, D. E., Downey, J. A. (1981). The evolutionary development of vertebrate thermoregulation. *Am. Sci.* 69: 543–550.
- de Lafontaine, Y., T. Lambert, G. R. Lilly, W. D. McKone, and R. J. Miller (eds.). 1992. Juvenile stages: the missing link in fisheries research. *Can. Tech. Rep. Fish. Aquat. Sci.* 1890, 137 p.
- Dew, C. B. (1976). A contribution to the life history of the cunner, Tautogolabrus adspersus, in Fishers Island Sound, Connecticut. *Chesapeake Sci.* 17: 101–113.
- Diana, J. S., MacKay, W. C., Ehrman, M. (1977). Movements and habitat preference of northern pike (Esox lucius) in Lac Ste. Anne, Alberta. *Trans. Am. Fish. Soc.* 106: 560–565.
- Doherty, P. J. (1982). Coral reef fishes: recruitment-limited assemblages? *Proc. Fourth Internat. Coral Reef Symp., Manila. Vol. 2:* 465–470.
- Doherty, P. J. (1983). Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology* 64: 176–190.

- Doherty, P. J. (1991). Spatial and temporal patterns in recruitment. In: P. F. Sale (ed.) *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego p. 261–293.
- Doherty, P. J., Williams, D. McB. (1988). The replenishment of coral reef fish populations. *Oceanogr. Mar. Biol. Ann. Rev.* 26: 487–551.
- Doherty, P. J., Fowler, A. J. (1994). An empirical test of recruitment limitation in a coral reef fish. *Science* 263: 935–939.
- Dreidzic, W. R., Hochachka, P. W. (1978). Metabolism in fish during exercise. In Hoar, W. S., Randall, D. J. (eds.) *Fish Physiology*. vol. VII, Academic Press, London. p. 503–543.
- Dunn, J. F. (1988). Low-temperature adaptation of oxidative energy production in cold-water fishes. *Can. J. Zool.* 66: 1098–1104.
- Eckert, G. J. (1985). Settlement of coral reef fishes to natural substrata at different depths. *Proc. Fifth Int. Coral Reef Congr., Tahiti*. Vol. 5: 131–139.
- Eckert, G. J. (1987). Estimates of adult and juvenile mortality for labrid fishes at One Tree Reef, Great Barrier Reef. *Mar. Biol.* 95: 167–171.
- Elliott, J. M. (1976). The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. *J. Anim. Ecol.* 45: 923–948.
- Forrester, G. E. (1990). Factors influencing the juvenile demography of a coral reef fish. *Ecology* 71: 1666–1681.
- Fry, F. E. J. (1947). Effects of the environment on animal activity. *Univ. Toronto Studies Biol. Ser.* 55. *Ont. Fish. Res. Lab.* 68: 1–62.

- Fry, F. E. J. (1971). The effect of environmental factors on the physiology of fish. In Hoar, W. S., Randall, D. J. (eds.) Fish Physiology, vol. VI. Academic Press, London. p. 1–98.
- Furnell, D. J. (1986). Partitioning of locomotor and feeding metabolism in sablefish (*Anaploma fimbria*). Can. J. Zool. 65: 486–489.
- Geiser, F. (1988). Reduction of metabolism during hibernation and daily torpor in mammals and birds: temperature effect or physiological inhibition? J. Comp. Physiol. 158B: 25–37.
- Gilliam, J. F., Fraser, D. F. (1987). Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68: 1856–1862.
- Goddard, S. V., Kao, M. H., Fletcher, G. L. (1992). Antifreeze production, freeze resistance, and overwintering of juvenile northern Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 49: 516–522.
- Goldstein, D. L. (1988). Estimates of daily energy expenditure in birds: the time–energy budget as an integrator of laboratory and field studies. Am. Zool. 28: 829–844.
- Gotceitas, V. (1990). Foraging and predator avoidance: a test of a patch choice model with juvenile bluegill sunfish. Oecologia 83: 346–351.
- Gotceitas, V., Brown, J. A. (1993). Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. Oecologia 93: 31–37.
- Haugaard, N., Irving, L. (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: 19–26.

- Hawkins, A. D., MacIennan, D. N., Urquhart, G. G., Robb, C. (1974). Tracking cod in a Scottish sea loch. *J. Fish Biol.* 6: 225–236.
- Hawkins, A. D., Urquhart, G. G., Smith, G. W. (1980). Ultrasonic tracking of juvenile cod by means of a large spaced hydrophone array. In Amlaner, C. J. Jr., MacDonald, D. W. (eds.) *A Handbook on Biotelemetry and Radio Tracking*. Pergamon Press, Oxford. p. 461–470.
- Heldmaier, G. (1989). Seasonal acclimatization of energy requirements in mammals: functional significance of body weight control, hypothermia, torpor and hibernation. In Wieser, W., Gnaiger, E. (eds.) *Energy Transformations in Cells and Organisms*. Georg Thieme Verlag, Stuttgart. p. 130–139.
- Helfman, G. S. (1978). Patterns of community structure in fishes: summary and overview. *Env. Biol. Fish.* 3: 129–148.
- Helfman, G. S. (1986). Fish behaviour by day, night and twilight. In Pitcher, T. J. (ed.) *The Behaviour of Teleost Fishes*. Croom Helm, London, p. 366–387.
- Henderson, P. A., Holmes, R. H. A., Bamber, R. N. (1988). Size-selective overwintering mortality in the sand smelt, *Atherina boyeri* Risso, and its role in population regulation. *J. Fish Biol.* 33: 221–233.
- Hertz, P. E., Huey, R. B., Garland, T. Jr. (1988). Time budgets, thermoregulation, and maximal locomotor performance: are reptiles Olympians or Boy Scouts? *Am. Zool.* 28: 927–938.
- Hixon, M. A. (1980). Food production and competitor density as the determinants of feeding territory size. *Am. Nat.* 115: 510–530.

- Hixon, M. A. (1991). Predation as a process structuring coral-reef fish communities. In Sale, P. F. (ed.) *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, p. 475-508.
- Hixon, M. A., Beets, J. P. (1989). Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bull. Mar. Sci.* 44: 666-680.
- Hixon, M. A., Beets, J. P. (1993). Predation, prey refuges and the structure of coral-reef fish assemblages. *Ecol. Monogr.* 63: 77-101.
- Hixon, M. A., Carpenter, F. L. (1988). Distinguishing energy maximizers from time-minimizers: a comparative study of two hummingbird species. *Am. Zool.* 28:
- Hobson, E. S. (1972). Activity of Hawaiian reef fishes during evening and morning transitions between daylight and darkness. *Fishery Bull. Fish Wildlif. Serv. U.S.*, 70: 715-740.
- Hobson, E. S. (1973). Diel feeding migrations in tropical reef fishes. *Helgolander wiss Meeresunters.* 24: 361-370.
- Hochachka, P., Somero, G. (1984). *Biochemical Adaptation*. Princeton Univ. Press, Princeton.
- Holbrook, S. J., Schmidt, R. J. (1988). The combined effects of predation risk and food reward on patch selection. *Ecology* 69: 125-134.
- Hoppeler, H., Turner, D. L. (1989). Plasticity of aerobic scope: adaptation of the respiratory system in animals, organs and cells. In Wieser, W., Gnaiger, E. (eds.) *Energy Transformations in Cells and Organisms*. Georg Thieme Verlag, Stuttgart. p. 116-122.

- Hoss, D. E., Coston-Clements, L., Peters, D. S., Tester, P. A. (1988). Metabolic responses of spot, Leiostomus xanthurus, and Atlantic croaker, Micropogonias undulatus, larvae to cold temperatures encountered following recruitment to estuaries. Fish. Bull. 86(3): 483–488.
- Houde, E. (1987). Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. Ser. 2: 17–29.
- Hunt von Herbing, I., Hunte, W. (1991). Spawning and recruitment of the bluehead wrasse, Thalassoma bifasciatum, in Barbados. Mar. Ecol. Prog. Ser. 72: 49–54.
- Hunte, W., Côté, I. M. (1989). Recruitment in the redlip blenny Ophioblennius atlanticus: Is space limiting? Coral Reefs 8: 45–50.
- Iwasa, Y., Roughgarden, J. (1984). Shoot/root balance of plants: optimal growth of a system with many vegetative organs. Theor. Pop. Biol. 25: 78–105.
- Jeffreys, A. J., Brookfield, J. F. Y., Semeneoff, R. (1985). Positive identification of an immigration test–case using human DNA fingerprints. Nature 317: 818–819.
- Jobling, M. (1980). Gastric evacuation in plaice, Pleuronectes platessa L: effects of dietary energy level and food consumption. J. Fish. Biol. 17: 187–196.
- Jobling, M. (1981). The influence of feeding on the metabolic rate of fishes: a short review. J. Fish. Biol. 18: 385–400.
- Jobling, M. (1985). Physiological and social constraints on growth of fish with special reference to Arctic charr, Salvelinus alpinus L. Aquaculture 44: 83–90.
- Johansen, F. (1925). Natural history of the cunner. Contrib. Can. Biol. 2: 423–468.

- Jones, G. P. (1984). The influence of habitat and behavioural interactions on the local distribution of the wrasse, Pseudolabrus celidotus. *Env. Biol. Fish.* 10: 43–58.
- Jones, G. P. (1986). Food availability affects growth in a coral reef fish. *Oecologia* 70: 136–139.
- Jones, G. P. (1987a). Competitive interactions among adults and juveniles in a coral reef fish. *Ecology* 68: 1534–1547.
- Jones, G. P. (1987b). Some interactions between residents and recruits in two coral reef fishes. *J. Exp. Mar. Biol. Ecol.* 114: 169–182.
- Jones, G. P. (1990). The importance of recruitment to the dynamics of a coral reef fish population. *Ecology* 71: 1691–1698.
- Jones, G. P. (1991). Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In Sale, P. F. (ed.) *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, CA. 754 pp.
- Juanes, F. (1994). What determines prey size selectivity in piscivorous fishes?, p. 79–100. In Storer, D. J., K. L. Fresh, and R. J. Feller (eds.). *Theory and Application Fish Feeding Ecology*. Belle W S. Carolina Press, Columbia, SC.
- Kaufman, L., Ebersole, J., Beets, J., McIvor, C. C. (1992). A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. *Env. Biol. Fish.* 34: 109–118.
- King, D., Roughgarden, J. (1982). Graded allocation between vegetation and reproductive growth for annual plants in growing seasons of random length. *Theor. Pop. Biol.* 22: 1–16.

- Koch, F., Wieser, W. (1983). Partitioning of energy in fish: can reduction in swimming activity compensate for the cost of production? *J. Exp. Biol.* 107: 141–146.
- Krebs, J. R., Davies, N. B. (1981). *An Introduction to Behavioural Ecology*. Blackwell, Oxford.
- Krebs, J. R., McCleery, R. H. (1984). Optimization in behavioural ecology. In Krebs, J. R., Davies, N. B. (eds.) *Behavioural Ecology. An Evolutionary Approach*. Blackwell, Oxford. p. 91–121.
- Larimore, R. W., Duever, M. J. (1968). Effects of temperature acclimation on the swimming ability of smallmouth bass fry. *Trans. Am. Fish. Soc.* 97: 175–184.
- Levin, P. S. (1991). Effects of microhabitat on recruitment variation in a Gulf of Maine reef fish. *Mar. Ecol. Prog. Ser.* 75: 183–189.
- Levin, P. S. (1993). Habitat structure, conspecific presence and spatial variation in the recruitment of a temperate reef fish. *Oecologia* 94: 176–185.
- Levin, P. S. (1994a). Fine-scale temporal variation in recruitment of a temperate demersal fish: the importance of settlement vs. post-settlement loss. *Oecologia* (in press).
- Levin, P. S. (1994b). Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply. *Env. Biol. Fish.* (in press).
- Li, H. W., Brocksen, R. W. (1977). Approaches to the analysis of intraspecific competition for space by rainbow trout (*Salmo gairdneri*). *J. Fish Biol.* 11: 329–341.

- Lomnicki, A. (1988). Population Ecology of Individuals. Princeton Univ. Press, Princeton.
- Lough, R. G., Valentine, P. C., Potter, D. C., Auditore, P. J., Bolz, G. Z., Neilson, J., Perry, R. I. (1989). Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. Mar. Ecol. Prog. Ser. 56: 1–12.
- Luckhurst, B. E., Luckhurst, K. (1977). Recruitment patterns of coral reef fishes on the fringing reefs of Curaçao, Netherlands Antilles. Can. J. Zool. 55:681–689.
- Magnuson, J. J. (1962). An analysis of aggressive behaviour, growth and competition for food and space in medaka (Oryzias latipes (Pisces, Cyprinodontidae)). Can. J. Zool. 40: 313–363.
- Malloy, K. D., Targett, T. E. (1991). Feeding, growth and survival of juvenile summer flounder, Paralichthys dentatus: experimental analyses of the effects of temperature and salinity. Mar. Ecol. Prog. Ser. 72: 213–223.
- Mapstone, B., Fowler, A. J. (1988). Recruitment and the structure of assemblages of fishes on coral reefs. Trends Ecol. Evol. 3(3): 72–77.
- Mattila, J. (1992). The effect of habitat complexity on predation efficiency of perch Perca fluviatilis L. and ruffe Gymnocephalus cernuus (L.). J. Exp. Mar. Biol. Ecol. 157: 55–67.
- McDonald, J. S., Dadswell, M. J., Appy, R. G., Melvin, G. D., Methven, D. A. (1985). Fishes, fish assemblages, and their seasonal movements in the lower Bay of Fundy and Passamaquoddy Bay, Canada. Fish. Bull. 82(1): 121–139.

- McFarland, W. N., Brothers, E. B., Ogden, J. C., Shulman, M. J., Bermingham, E. L., Kotchian-Prentiss, N. M. (1985). Recruitment patterns in young French grunts, Haemulon flavolineatum (Family Haemulidae), at St. Croix, Virgin Islands. Fish. Bull. 83(3): 413–426.
- Medley, P. A., Gaudian, G., Wells, S. (1993). Coral reef fisheries stock assessment. Rev. Fish Biol. Fish. 3: 242–285.
- Milicich, M. J., Meekan, M. G., Doherty, P. J. (1992). Larval supply: a good predictor of recruitment of three species of reef fish (Pomacentridae). Mar. Ecol. Prog. Ser. 86: 153–166.
- Muir, B. S., Niimi, A. J. (1972). Oxygen consumption of the euryhaline fish aholehole (Kuhlia sandvicensis) with reference to salinity, swimming, and food consumption. J. Fish. Res. Bd. Can. 29: 67–77.
- Munro, J. L. (1983). Caribbean Coral Reef Fishery Resources. ICLARM Stud. Rev. 7: 1–276.
- Olla, B. L., Bejda, A. J., Martin, A. D. (1975). Activity, movements, and feeding behaviour of the cunner, Tautogolabrus adspersus, and comparison of food habits with young tautog, Tautoga onitis, off Long Island, New York. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 73: 895–900.
- Olla, B. L., Bejda, A. J., Martin, A. D. (1979). Seasonal dispersal and habitat selection of cunner Tautogolabrus adspersus, and young tautog, Tautoga onitis, in Fire Island Inlet, Long Island, New York. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 77: 255–261.

- Paul, A. J., Paul, J. M., Smith, R. L. (1990). Rates of oxygen consumption of yellowfin sole (Limanda aspera (Pallas)) relative to body size, food intake, and temperature. J. Cons. int. Explor. Mer 47: 205–207.
- Pearson, O. P. (1954). The daily energy requirements of a wild Anna hummingbird. Condor 56: 317–322.
- Pianka, E. R. (1976). Natural selection of optimal reproductive tactics. Am. Zool. 16: 775–784.
- Polovina, J. J., Ralston, S. (1986). An approach to yield assessment for unexploited resources with application to the deep slope fishes of the Marianas. Fish. Bull. U.S. 84: 759–770.
- Pottle, R. A., Green, J. M. (1979). Field observations on the reproductive behaviour of the cunner, Tautogolabrus adspersus (Walbaum), in Newfoundland. Can. J. Zool. 59: 1582–1585.
- Post, J. R., Evans, D. O. (1989a). Experimental evidence of size-dependent predation mortality in juvenile yellow perch. Can. J. Zool. 67: 521–523.
- Post, J. R., Evans, D. O. (1989b). Size-dependent overwinter mortality of young-of-the-year yellow perch (Perca flavescens): laboratory, in situ enclosure, and field experiments. Can. J. Fish. Aquat. Sci. 46: 1958–1968.
- Priede, I. G. (1985). Metabolic scope in fishes. In Tytler, P., Calow, P. (eds.) Fish Energetics: New Perspectives. Croom Helm, London. p. 33–64.
- Randall, D. J., Daxboeck, C. (1982). Cardiovascular changes in the rainbow trout (Salmo gairdneri Richardson) during exercise. Can. J. Zool. 60: 1135–1140.

- Roberts, C. M., Ormond, R. G. (1987). Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar. Ecol. Prog. Ser.* 41: 1–8.
- Roberts, C. M., Polunin, N. V. C. (1991). Are marine reserves effective in management of reef fisheries? *Rev. Fish Biol. Fish.* 1: 65–91.
- Robertson, D. R. (1988a). Abundances of surgeonfishes on patch-reefs in Caribbean Panama: due to settlement, or post-settlement events? *Mar. Biol.* 97: 495–501.
- Robertson, D. R. (1988b). Settlement and population dynamics of Abudefduf saxatilis on patch reefs in Caribbean Panama. *Proc. Sixth Int. Coral Reef Symp.* 2: 839–843.
- Roff, D. A. (1983). An allocation model of growth and reproduction in fish. *Can. J. Fish. Aquat. Sci.* 40: 1395–1404.
- Sale, P. F. (1977). Maintenance of high diversity in coral reef fish communities. *Am. Nat.* 111: 337–359.
- Sale, P. F. (1978). Coexistence of coral reef fishes – a lottery for living space. *Environ. Biol. Fishes* 3: 85–102.
- Sale, P. F. (1991). Reef fish communities: open nonequilibrium systems. In: Sale PF (ed) *The Ecology of Fishes on Coral Reefs*. Academic Press, Inc. San Diego, California, pp 564–598.
- Sale, P.F., Douglas, W. A., Doherty, P. J. (1984). Choice of microhabitats by coral reef fishes at settlement. *Coral Reefs* 3: 91–99.
- Sale, P. F., Ferrell, D. J. (1988). Early survivorship of juvenile coral reef fishes. *Coral Reefs* 7: 117–124.

- Schaffer, W. M., Inouye, R. S., Whittam, T. S. (1982). The dynamics of optimal energy allocation for an annual plant in a seasonal environment. *Am. Nat* 120: 787–815.
- Schartz, R. L., Zimmerman, J. L. (1971). The time and energy budget of the male dickcissel (*Spiza americana*). *Condor* 73: 65–76.
- Schoener, T. W. (1971). Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2: 369–404.
- Scott, W. B., Scott, M. G. (1988). Atlantic Fishes of Canada. *Can. Bull. Fish. Aquat. Sci.* 219: 1–731.
- Shulman, M. J. (1984). Resource limitation and recruitment patterns in a coral reef fish assemblage. *J. Exp. Mar. Biol. Ecol.* 74: 85–109.
- Shulman, M. J. (1985a). Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* 66: 1056–1066.
- Shulman, M. J. (1985b). Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* 68: 1056–1066.
- Shulman M. J., Ogden J. C., Ebersole J. P., McFarland W. N., Miller S. L., Wolf N. G. (1983). Priority effects in the recruitment of juvenile coral reef fishes. *Ecology* 64: 1508–1513.
- Shulman, M. J., Ogden, J. C. (1987). What controls tropical reef populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. *Mar. Ecol. Prog. Ser.* 39: 233–242.
- Shuter, B. J., Wisner, D. A., Reiger, H. A., Matuszek, J. E. (1985). An application of ecological modelling: impact of thermal effluent on a smallmouth bass population. *Trans. Am. Fish. Soc.* 114: 631–651.

- Sibly, R. M., Calow, P. (1986). *Physiological Ecology of Animals*. Blackwell, Oxford.
- Smith, C. L. (1978). Coral reef fish communities: a compromise view. *Env. Biol. Fish.* 3(1): 109–128.
- Smith, C. L., Tyler, J. C. (1972). Space resource sharing in a coral reef fish community. In Collette, B. B., Earle, S. A. (eds.) *Results of the Tektite program: ecology of coral reef fishes*. Los Ang. Co. Mus. Sci. Bull. 14: 125–170.
- Sogard, S. (1992). Variability in growth rates of juvenile fishes in different estuarine habitats. *Mar. Ecol. Prog. Ser.* 85: 35–53.
- Sokal, R. R., Rohlf, F. J. (1981). *Biometry*. Second ed. Freeman, San Francisco, CA. 859 p.
- Soofiani, N. M., Hawkins, A. D. (1982). Energetic costs at different levels of feeding in juvenile cod, Gadus morhua L. *J. Fish Biol.* 21: 577–592.
- Soofiani, N. M., Priede, I. G. (1985). Aerobic metabolic scope and swimming performance in juvenile cod, Gadus morhua L. *J. Fish Biol.* 26: 127–138.
- Stiles, F. G. (1971). Time, energy and territoriality of the Anna hummingbird (Calypte anna). *Science* 173: 818–821.
- Storey, K. B., Storey, J. M. (1990). Metabolic rate depression and biochemical adaptation in anaerobiosis, hibernation and estivation. *Quart. Rev. Biol.* 65: 145–174.
- Swain, D. P., Wade, E. J. (1993). Density-dependent geographic distribution of Atlantic cod (Gadus morhua) in the southern Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* 50: 725–733.

- Sweatman, H. (1985). The influence of adults of some coral reef fishes on larval recruitment. *Ecol. Monogr.* 55: 469–85.
- Sweatman, H. (1988). Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. *J. Exp. Mar. Biol. Ecol.* 124: 163–174.
- Tang, Y., Nelson, J. A., Reidy, S. P., Kerr, S. R., Boutilier, R. G. (1994). A reappraisal of activity metabolism in Atlantic cod (Gadus morhua). *J. Fish Biol.* 44: 1–10.
- Thresher, R. E. (1983). Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef lagoon. *Mar. Ecol. Prog. Ser.* 10: 137–145.
- Tupper, M., Boutilier, R. G. (1992). Settlement and growth of age 0+ cod (Gadus morhua) in St. Margaret's Bay, Nova Scotia. *Can. Tech. Rep. Fish. Aquat. Sci.* 1890: 89–90.
- Tupper, M., Boutilier, R. G. (1994). Size and priority influence growth and competitive success of newly settled Atlantic cod. *Mar. Ecol. Prog. Ser.* (in press).
- Tupper, M., Hunte, W. (1994). Recruitment dynamics of coral reef fishes in Barbados. *Mar. Ecol. Prog. Ser.* (in press).
- Vahl, O., Davenport, J. (1979). Apparent specific dynamic action of food in the fish Blennius pholis. *Mar. Ecol. Prog. Ser.* 1: 109–113.
- Verbeek, N. A. M. (1964). A time and energy budget study of the brewer blackbird. *Condor* 66: 70–74.
- Victor, B. C. (1982). Daily otolith increments and recruitment in two coral-reef wrasses, Thalassoma bifasciatum and Halichoeres bivittatus. *Mar. Biol.* 71: 203–208.

- Victor, B. C. (1982). Daily otolith increments and recruitment in two coral-reef wrasses, Thalassoma bifasciatum and Halichoeres bivittatus. Mar. Biol. 71: 203-208.
- Victor, B. C. (1983). Recruitment and population dynamics of a coral reef fish. Science 219: 419-420.
- Victor, B. C. (1986). Delayed metamorphosis with reduced larval growth in a coral reef fish, Thalassoma bifasciatum. Can. J. Fish. Aquat. Sci. 43: 1208-1213.
- Victor, B. C. (1991). Settlement strategies and biogeography of reef fishes. Pages 231-260 in P. F. Sale (ed.), The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, CA.
- Walsh, W. J. (1985). Reef fish community dynamics on small artificial reefs: the influence of isolation, habitat, structure, and biogeography. Bull Mar Sci 39: 357-376.
- Walsh, W. J. (1987). Patterns of recruitment and spawning in Hawaiian reef fishes. Env. Biol. Fish. 18: 257-276.
- Walters, C. J., Juanes, F. (1994). Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Can. J. Fish. Aquat. Sci. (in press).
- Ware, D. M. (1982). Power and evolutionary fitness of teleosts. Can. J. Fish. Aquat. Sci. 39: 3-13.
- Warner, R. R., Hughes, T. P. (1988). The population dynamics of reef fishes. Proc. Sixth Int. Coral Reef Symp. 1: 149-155.

- Watt, W. B. (1986). Power and efficiency as indexes of fitness in metabolic organization. *Am. Nat.* 127(5): 629-653.
- Weatherley, A. H., Gill, H. S. (1987). *The Biology of Fish Growth*. Academic Press, London.
- Werner, E. E., and D. J. Hall. (1988). Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69: 1352-1366.
- Whoriskey, F. G. (1983). Intertidal feeding and refuging by cunners, Tautogolabrus adspersus (Labridae). *U.S. Fish. Bull.* 81: 426-428.
- Wicklund, R. I. (1970). Observations on the spawning of cunner in waters of northern New Jersey. *Chesapeake Sci.* 11: 137.
- Wieser, W. (1989). Energy allocation by addition and by compensation: an old principle revisited. In Weiser, W., Gnaiger, E. (eds.), *Energy Transformations in Cells and Organisms*. Georg Thieme Verlag, Stuttgart. p. 98-105.
- Wilkinson, W. 1990. *SYSTAT: The System for Statistics*. Systat, Inc., Evanston, Ill.
- Wolf, L. L., Hainsworth, F. R. (1971). Time and energy budgets of territorial hummingbirds. *Ecology* 52: 980-988.
- Wootton, R. J. (1990). *Ecology of Teleost Fishes*. Chapman and Hall, London. 404 p.
- Zar, J. H. (1984). *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs. 718 p.